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A STUDY OF THE SHARKS OF THE SUBORDER SQUALOIDEA

By Henry B. Bigelow and William C. Schroeder

With Four Plates

CAMBRIDGE, MASS., U. S. A.
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No. 1 — *A Study of the Sharks of the Suborder Squaloidea*[1]

By Henry B. Bigelow and William C. Schroeder

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[1] Contribution 848, Woods Hole Oceanographic Institution.

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FOREWORD

The sharks that lack an anal fin but do have snouts of the ordinary "shark" form, and pectoral fins that are wholly posterior to the gill openings (grouped together here as the suborder Squaloidea), have been surveyed of late for Philippine waters and adjacent seas by Fowler (1941) and for the western North Atlantic by Bigelow and Schroeder (1948). But the most recent comprehensive accounts of the group for the oceans as a whole, by Regan (1908) and by Garman (1913, pp. 188-244), now lie many years in the past. And so much additional information has come to hand during these years, from various sources, that the time seems ripe for a fresh survey of the group. Many taxonomic questions, however, still await for their solution the critical examination of large series of specimens. We attempt little more in the following pages than to summarize the present state of knowledge of the group. Anything as ambitious as would be implied by the word "revision" is a task for the future.

It will save repetition if we state here (once and for all) that the names of the species we have seen are preceded by an asterisk (*).

Also, we should remind the reader, who may not be familiar with the use of the trawl in deep water, that the depths of capture reported by this method, under the several genera, are in reality those at which the trawl was dragging on the bottom. This is not necessarily the depth at which the shark in question was living, for it is always possible that any particular specimen (even of the species that hold closest to the bottom) may have been picked up when the trawl was being lowered, or hauled up again through the water. The only precise data in this regard are for specimens caught on hook and line. And we have very few definite records of depths of capture for line-caught sharks.

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We welcome the opportunity of thanking our colleagues in different parts of the world who have assisted us in various ways: especially Dr. Tokiharu Abe, Tokyo, for contributing a specimen of *Somniosus longus;* the Australian Museum, through Dr. G. P. Whitley, for a specimen of *Oxynotus bruniensis;* Dr. G. Belloc of the Museum, Monaco, for the gift of an excellent specimen

of *Oxynotus* from Italy; Dr. James Böhlke, of the Academy of Natural Sciences for making available to us for study the type specimen of *Heteroscymnoides marleyi,* from the Natal Coast, southern Africa; the British Museum for the loan of the specimens of *Centroscymnus crepidater* and of *Scymnodon ringens,* on which Günther (1870) based his descriptions of these species, and of a specimen of *Oxynotus paradoxus;* Dr. Paul Budker, of the Paris Museum, for denticles from the type specimen of *Scymnodon obscurus,* and for drawings of its teeth; Dr. Fernando Frade for re-examining for us the type specimen of *Oxynotus paradoxus;* Dr. Arni Fridriksson for specimens of *Centrophorus squamosus* and of *Somniosus microcephalus* from Iceland; Dr. J. A. F. Garrick for kindly allowing us to quote from his manuscripts in advance of publication, for a specimen of a New Zealand shark apparently not separable from *Centroscymnus crepidater* of the eastern North Atlantic and for a paratype of *Etmopterus abernathyi*; Dr. Finnur Gudmundsson, of the Museum of Natural History, Reykjavik, for the loan of an excellent series of *Centroscymnus crepidater* (see p. 91); Col. John K. Howard for specimens of *Squalus megalops* from New South Wales; Mr. N. B. Marshall for notes on *Euprotomicrus* (p. 127); Dr. George S. Myers, of the Natural History Museum, Stanford University, for loaning us a paratype of *Centroscyllium ruscosum;* Mr. G. Palmer, of the British Museum, for contributing tracings of pectoral fins of Richardson's young specimen of *Acanthias vulgaris,* renamed *Squalus megalops* by Regan; Dr. J. R. Pfaff, University Zoological Museum, Copenhagen, for the loan of specimens of *Centrophorus squamosus, Deania calcea,* and *Centroscymnus crepidater,* from Icelandic waters, and for the gift of a specimen of *C. crepidater;* Dr. A. M. Ramalho for many kindnesses, including the contribution of a series of *Oxynotus centrina* from off Portugal and of an excellent specimen of *Echinorhinus brucus* from northwest Africa, also for photographs of a specimen (now in the Bocage Museum in Lisbon) that had been described and pictured in 1870 by Capello under the name *Lacmargus rostratus* Risso 1826; Dr. Leonard Schultz, for making available to us the extensive collections of the U. S. National Museum, as well as for assistance in various other ways; Dr. J. L. B. Smith, Rhodes University, Grahamstown, for photographs of the second dorsal fin spine of the shark described by Gilchrist

1922 as *Atractophorus armatus;* Dr. Ethelwyn Trewavas of the British Museum for contributing a drawing of a lower tooth of the type specimen of *Centroscymnus macracanthus* as well as for constant cooperation; Mr. Denys W. Tucker of the British Museum for drawings of the first and second dorsal fins of the type specimen of *Centroscymnus macracanthus;* and Dr. Gilbert P. Whitley, of the Australian Museum, for making available to us a lower tooth from the type specimen of *Centrophorus harrisonii* and for contributing a tracing of the pectoral fins of the type specimen of *Squalus megalops.*

Drawings are by Eugene N. Fischer, Jessie H. Sawyer and Henry B. Bigelow, except as otherwise noted. Photographs were contributed by the Woods Hole Oceanographic Institution.

CLASSIFICATION OF THE SQUALOIDEA

While the sharks in question are an extremely homogeneous assemblage differing conspicuously in their general makeup from the other groups of sharks with which they share the lack of an anal fin (pristiophoroids and squatinoids), the taxonomic ranking assigned to them by recent authors has reflected divergent viewpoints. Thus they have been grouped with the pristiophoroids by Garman (1913, pp. 12, 13) as the "group of families" Squaloidei; by Berg (1940; Eng. Trans. 1947, p. 381) as the suborder Squaloidei; by White (1937, pp. 100, 101) as the suborder Squalida; and by Bertin (1939, pp. 17-19) as the suborder Squaliformes. Fowler (1941, pp. 222, 279) has placed the squaloids in a separate order (Cyclospondyli), joining the pristiophoroids with the squatinoids as the order Squatinae. Bigelow and Schroeder (1948, p. 77) classed the squaloids as one suborder (Squaloidea), the pristiophoroids as a second suborder (Pristiophoroidea), and the squatinoids as a third suborder (Squatinoidea) of the order Selachii. Still more recently Berg, 1955, while similarly classifying the squaloids and the squatinoids as suborders, has set the pristiophoroids apart as a separate order. And this arrangement has much to recommend it for the pristiophoroids are distinguished not only by their sawlike snout, but by the "presence of a separate antorbital bar, from which the upper jaw is suspended by a broad ligament, in addition to the articulation to the cranium" (Bigelow and Schroeder, 1948, p. 532).

Characters. Sharks without an anal fin, but with the snout of the ordinary shape (i.e. not beak-like and without lateral teeth or cirri), and subcylindrical in general form, the anterior margins of the pectoral fins not expanded forward past the first pair of gill openings. Two dorsal fins, with or without fin-spines. Only 5 gill openings, all of them anterior to the pectorals. Inner margins of pelvics entirely separate posterior to cloaca. Nostrils entirely separate from mouth. Spiracles present and conspicuous. Eyes without nictitating fold or membrane. (For internal characters, see Bigelow and Schroeder, 1948, p. 449.)

Families. Views have differed as to whether a subdivision of the Squaloidea into separate families is justified on any basis that has yet been proposed. Garman (1913, p. 13) distributed them among three families: Squalidae for those with spines in the dorsal fins, Scymnorhinidae and Echinorhinidae for those without spines, separating these last two, one from the other, by differences in their teeth. And this same scheme was accepted by Bigelow and Schroeder (1948, p. 450), except that they replaced the name Scymnorhinidae by Dalatiidae because the generic name *Scymnorhinus* Bonaparte 1846 is synonymous with *Dalatias* Rafinesque 1810. Bertin (1939), however, recognized only two families among the sharks in question — Squalidae for those with fin spines, and Scymnorhinidae for those without spines — while Berg (1940) has united them all in the single family Squalidae. And Hubbs and McHugh (1951, pp. 163, 164), for the reasons stated on p. 9, follow Berg in their suggestion "that the Dalatiidae be fused with Squalidae" and that the Echinorhinidae "should likewise be synonymized with Squalidae," though they retain the Dalatiinae and Echinorhininae as subfamilies, pending future study.

These differences do not stem from any recent increase in factual knowledge, for the external features of the squaloid sharks were about as well known structurally a hundred years ago as they are today. What the different systems do chiefly mirror is the opinions held by the several authors as to the degrees of consanguinity among the animals in question. The expression, however, of views in this regard is but the secondary purpose of animal classification; the primary purpose, as so trenchantly worded by Simpson (1945, p. 13), is to "provide a convenient practical means by which zoologists may know what

they are talking about and others may find out." In the case of any suborder as homogeneous structurally as the squaloid sharks are, and for which the fossil record throws little light on their evolutionary history, the decision, whether any subdivision into different families is warranted depends primarily (in our opinion) on whether it will help anyone from the practical standpoint. The scheme adopted here is based on this premise. At the same time it also emphasizes the strong probability that one of the genera with which we are here concerned (*Oxynotus*) represents a separate line of descent, for it is set apart from all the others not only by the arrangement of its upper teeth, by the nature of its dermal denticles, and by its body form (p. 14), but also because it was differentiated at least as early as the Miocene.

Oxynotus was made the basis of a separate family (Oxynotidae) by Jordan (1923, p. 103), followed by Rey (1928, p. 467).[2] And this course is followed here, as better indicative of the apparent degrees of genetic relationship among squaloid genera than was our former inclusion of it in the family Squalidae (Bigelow and Schroeder, 1948, p. 450).

The Linnean genus *Squalus*, which includes the common spiny dogfishes, has been regarded as what may be termed the "key genus" among the squaloids that remain after the subtraction of *Oxynotus*. This implies that the ancestors of the modern squaloids had spines in their dorsal fins. And this view, recently urged by Hubbs and McHugh (1951), is at least consistent with the fossil record, for *Protospinax* Woodward 1919, from the Upper Jurassic of Bavaria, with a spine of the squaloid type in each of its dorsal fins, but with a small anal fin (if Woodward's interpretation of the specimen be correct), and with teeth but little differentiated in nature, may in some measure bridge the gap between the squaloid sharks and the galeoids. Hubbs and McHugh further argue that the absence of a spine in the second dorsal fin in such of the sharks in question as lack one (also of a spine in the first dorsal fin in all but one of the genera in question) probably does not point to any close relationship among them, but more likely represents the end result of convergent evolution (i.e. loss of fin spines) along separate phyletic lines leading back to as many separate spiny-finned ancestors. As one illustration, they point out that "com-

[2] Regarded as a subfamily by Fowler, 1941, p. 223.

plete obsolescence of the spines would render *Centroscymnus* scarcely separable from *Somniosus.*" This leads them to conclude that the presence or absence of spines in the dorsal fins has been given undue weight in current classifications of the squaloid sharks (as by Bigelow and Schroeder, 1948) in which it is invoked as the basis for the separation of families. Here the fossil record does not help us at all, for this reaches as far back for the genera *Dalatias* and *Isistius,* which lack fin spines, as for the spiny-finned genera *Squalus, Etmopterus* and *Centrophorus,* i.e. to the Upper Cretaceous — always provided that identification of the fossils in question with these modern genera was correct. For that matter, a shark with a rostral blade (but lacking rostral teeth) that may reasonably be regarded as ancestral to the pristiophoroids (Woodward 1932, p. 476, Pl. 18; see also Jaekel, 1890, for other early pristiophorid fossils) is similarly known from the Upper Cretaceous; *Squatina* is even known from as far back as the Jurassic. Thus both the squaloids with spiny fins and those lacking spines, the progenitors of the pristiophoroids with their bizarre snouts, and the squatinoids (ray-like in appearance though true sharks) had completed their major evolutionary history by the Upper Cretaceous period, which (the geologists tell us) lies something like 75 million years in the past. For all that is known to the contrary, this may equally apply to the aberrant squaloid genera *Oxynotus* and *Echinorhinus,* though the known record for these runs back only to the Miocene. (For the fossil record of modern shark genera, see Romer 1945, pp. 576-577.)

Were one approaching the problem anew, the shape of the caudal fin, combined with the degree of elevation of the caudal axis, would seem about as appropriate as would the presence or absence of fin spines for a primary alternative among the genera of squaloids. Thus the one character is about as susceptible of precise determination as the other, while, in each case, the extreme states are bridged by intermediates so that division is not sharp-cut on either basis. Also the use of either one would result in the same grouping of genera as would the use of the other, with one exception.

A third character that is alternative between the groups of genera under discussion here, though it seems not to have been emphasized previously in this particular connection, is the con-

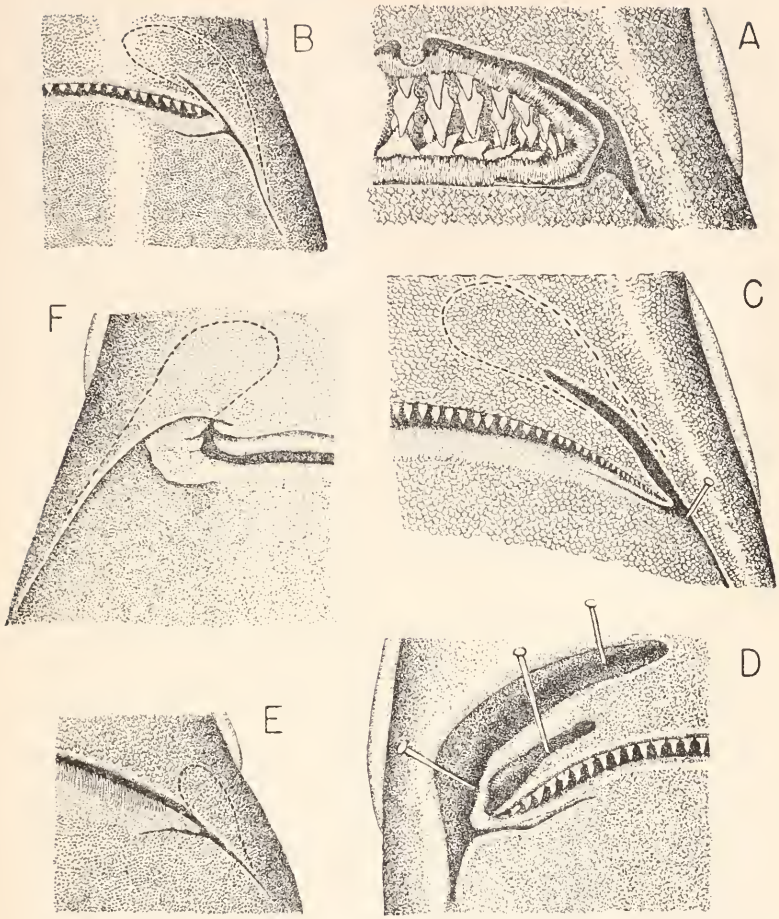

Fig. 1. Corner of mouth, of different squaloids, to show preoral clefts and preoral pouches, if any; the latter outlined by the broken curves. A, *Oxynotus centrina*, male 590 mm. long, Mus. Comp. Zool. No. 39576, x about 3. B, *Centrophorus squamosus*, female 1230 mm. long, Iceland, Mus. Comp. Zool. No. 37825, x about 0.5. C, *Centroscymnus coelolepis*, female, 1035 mm. long, offing of Delaware Bay, Mus. Comp. Zool. No. 38295, x about 2. D, *Centroscymnus crepidater*, female, 784 mm. long, Faroes, Mus. Comp. Zool., No. 39577, with preoral cleft and upper labial furrow pinned open, x about 1. E, *Dalatias licha*, male, 1114 mm. long, Japan, Mus. Comp. Zool. No. 1116, x about 0.5. F, *Isistius brasiliensis*, female, 501 mm. long, Japan, Mus. Comp. Zool. No. 1245, x about 2.

formation of the more or less voluminous inpocketing of the lower surface of the head, that bounds each angle of the jaw on the outer side. In all the known genera of Squaloidea that have a spine in the second dorsal fin as well as in the first (including *Oxynotus,* Fig. 1A), this oral pocket extends inward-forward across the lower surface of the head, anterior to the upper jaw, as an open and conspicuous preoral cleft, that is simple in some (e.g. *Oxynotus,* Fig. 1A; *Centroscymnus crepidater,* Fig. 1D), but that expands inwardly in most to form a more or less voluminous subdermal pouch (e.g. in *Centroscymnus coelolepis,* Fig. 1C). On the other hand, the majority of the genera that lack a spine in the second dorsal fin equally lack the open preoral cleft, although the preoral pouch extending forward from each of the oral pockets is voluminous (Fig. 1E, F). Two, however, of the genera of this group, *Scymnodalatias* and *Echinorhinus* do have short preoral clefts.

And, in any case, the group difference in this respect, while a convenient aid in the definition and identification of genera, is obviously of the kind rated by White (1937, pp. 51-53) as of "physiological importance," rather than as an indication of lines of ancestral descent.

There seems, in short, to be "no securely objective basis," as pointed out by Hubbs and McHugh (1951, p. 163) "on which to choose between the characters to be emphasized" in the classification of the Squaloidea.

But the cause of stability in nomenclature seems best served by using the presence or absence of fin spines as the primary alternative, since this accords with precedent, whereas to use the shape of the caudal fin, as have Hubbs and McHugh (1951, p. 164) in their analytical key to the dalatiine sharks, or to emphasize the presence or absence of the preoral clefts, would result in a novel alignment which we could not support by any cogent reasoning. But we wish it understood that this choice does not carry any phylogenetic implication but is purely a matter of convenience.

In our earlier synopsis of the Squaloidea (Bigelow and Schroeder 1948, p. 450), we recognize two families for such of the genera as lack a fin spine in the second dorsal fin: Dalatiidae for those in which the teeth have only one cusp, but are of conspicuously different shapes in the two jaws, contrasted with

Echinorhinidae (for *Echinorhinus*), in which the teeth are similar in the two jaws, with several cusps. But it seems more logical, in view of the uncertainties just discussed, to follow Hubbs and McHugh (1951) in reducing these categories to the rank of subfamilies of the family Squalidae, the structural contrast between them obviously being much narrower than that between either of them and the genus *Oxynotus* (p. 14).

Key to Families of Squaloidea

Only two or three upper teeth in the first row, but with the number of teeth greater by one in each successive row, so that the rows of functional teeth are successively longer from front to rear; trunk subtriangular in cross section with a prominent ridge low down on either side anterior to the pelvic fins ..... Family Oxynotidae, p. 13

About as many upper teeth in the anterior row as in the succeeding rows, so that any one functional row is about as long as any other; trunk subcylindrical in cross section in most; longitudinal ridges, if any, confined to the tail sector posterior to the pelvic fins ..... Family Squalidae, p. 17

Family OXYNOTIDAE

Family characters (based on only known genus, *Oxynotus*). Squaloidea with the upper teeth occupying a triangular area on the roof of the mouth, in quincuncial arrangement, the functional rows successively longer from front to rear, the first row consisting of three teeth only (on specimen studied, two, according to Rey 1928, p. 469), the number of teeth greater by one in each successive row, and with about six rows functional; lower teeth in a single functional row, blade-like, the median tooth symmetrically triangular, but the successive teeth increasingly oblique, outward (Pl. 1); the uppers smooth-edged, but the lowers finely serrate. The trunk subtriangular in cross section, with a prominent longitudinal ridge low down on either side anterior to the pelvic fins; preoral clefts well developed and very conspicuous, extending forward-inward so far that they are separated by only a narrow isthmus in the midline of the snout (Fig. 1A); lips thick, spongy, with a complex series of cross folds (Fig.

1A); first dorsal fin spine slanting either rearward or forward;[3] the first dorsal fin either with or without supporting radial cartilages posterior to the imbedded portion of the spine; both fin spines conspicuously stout, but projecting only slightly beyond the skin. Dermal denticles so large and prominent that the skin is very rough. On young specimens they are tridentate, with the median point much the longest. But they are much more complex in form on adults, mostly with three subsidiary points, the basal point with a varying number of radial furrows (for excellent illustrations of the denticles, see Rey 1928, p. 471, Fig. 157).

Genera. Only one genus is known: *Oxynotus* Rafinesque 1810.

Remarks. The pattern in which its upper teeth are arranged sets *Oxynotus* apart from all other squaloid sharks — from all other sharks for that matter — which of itself seems to us warrant enough for referring it to a separate family.

Genus OXYNOTUS Rafinesque 1810

Oxynotus Rafinesque, 1810, pp. 45, 60, type species **Squalus centrina* Linnaeus 1758, p. 233, type locality, Mediterranean. For generic synonyms, see Garman, 1913, p. 190.

Generic characters. Those of the family (p. 13). Maximum length probably not far from one meter.

Depth range. The type species (*centrina*) has attracted scientific attention at least since the time of Belon (1515, p. 46 bis), and is well known to Mediterranean fishermen, in moderately deep water. But the only definite statements we have found as to depth of capture are Roule's (1919, p. 123) report of a Mediterranean specimen taken at 60 meters, and Poll's (1951, p. 57) report of three, from 100-180 meters off equatorial West Africa. Depth records for the newly discovered **O. paradoxus* (p. 16) have ranged between 265 and 530 meters (Tucker and Palmer 1949, p. 930). All we have found for **bruniensis* of the Australian-New Zealand region is that a specimen at hand (p. 5) was trawled at about 180 meters.

[3] This seems an appropriate place to remind the reader that it is only the first dorsal fin spine that is inclined forward in any known species of *Oxynotus*, not both of the fin spines, as is erroneously stated in our earlier key to the genera of Squalidae (Bigelow and Schroeder 1948, p. 450, alternative 1A); also that in constructing that key we had overlooked the conditions existing in **O. paradoxus*.

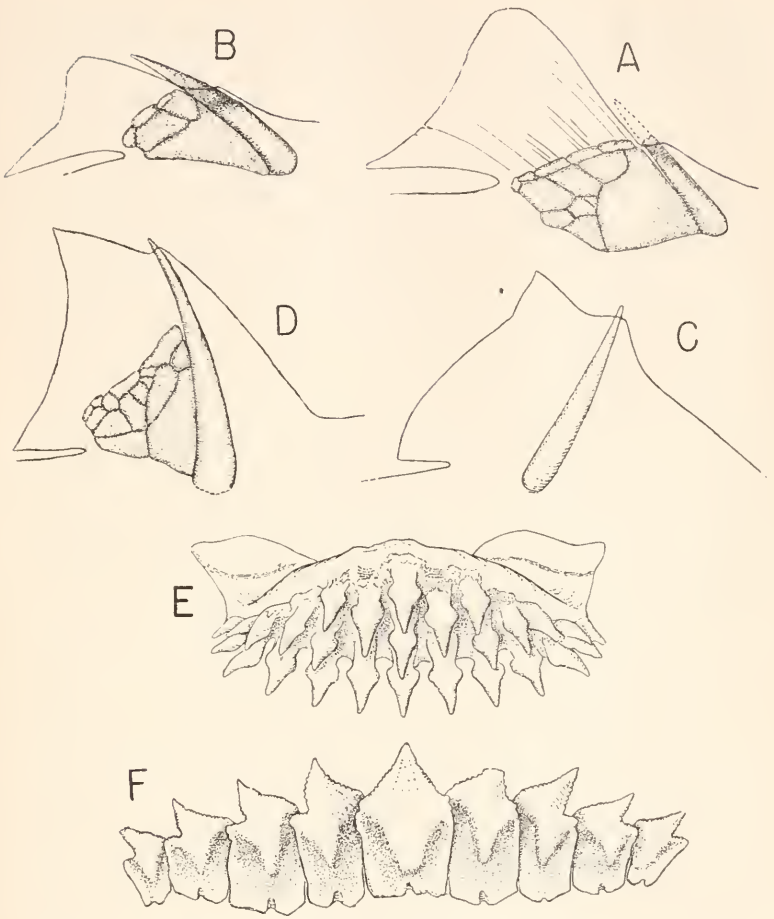

Fig. 2. A, dissection of first dorsal fin of *Squalus acanthias*, female, about 800 mm. long, coast of Massachusetts, Mus. Comp. Zool. No. 458, x about 0.5, to show radial cartilages. B, similar dissection of second dorsal fin of same. C, similar dissection of first dorsal fin of female *Oxynotus centrina*, 640 mm. long, Mediterranean (Mus. Comp. Zool. No. 39564), x about 0.5; D, similar dissection of second dorsal fin of same, x about 0.5; E, *Oxynotus centrina*, male, 590 mm. long, Mus. Comp. Zool. No. 39576, upper jaw and teeth, viewed from in front, x about 3.3; F, lower teeth of same, functional row, viewed from outside the mouth, x about 3.8.

Remarks. Previous to 1929 it had been generally agreed that the forward inclination of the first dorsal fin spine in the two species of *Oxynotus* that had been described up to that time was (with the arrangement of the upper teeth) diagnostic of the genus *Oxynotus,* which still remains the only known representative of the family Oxynotidae. But Frade's discovery in 1929 that the first dorsal spine in his new species **O. paradoxus,* from the coast of Morocco, is inclined rearward (see also Frade 1932 and Norman 1932) has shown that the direction in which it slopes can no longer be regarded as a generic alternative here.

Species. Three species are known: (1) **centrina* (Linnaeus) 1758, familiar to fishermen in the Mediterranean and neighboring parts of the eastern North Atlantic, ranging northward regularly to the Bay of Biscay, also known as a stray to Cornwall (Day 1880-1884, p. 319) and to Norway (Jenkins 1925, p. 321); (2) **bruniensis* (Ogilby) 1893, originally described from Tasmania and subsequently reported from southern Australian waters and from New Zealand; and (3) **paradoxus* Frade 1929, eastern North Atlantic between Morocco and Ireland. For excellent accounts and illustrations of the newly discovered **O. paradoxus,* see Frade 1932 and Norman 1932.

The most conspicuous respects in which these three differ externally one from another are in the shapes of the dorsal fins and in the direction in which the first dorsal spine is slanted. For details we refer the reader to Norman's (1932) illustration and key. A more interesting morphologic difference is that while in **paradoxus* and in **bruniensis* the first dorsal fin posterior to the spine is supported, as in *Squalus* (Fig. 2A, B), by a series of radial cartilages, in **centrina* (Fig. 2C, D) the first dorsal fin has no radial cartilages but is supported solely by the spine.

The dentition also differs in detail from species to species in *Oxynotus,* as is so commonly the case in other genera of sharks. Thus the upper teeth, which are narrow-awl-shaped in the central rows but broadly triangular and blade-like in the outer rows in **centrina* (Pl. 1), are relatively broader in the central rows but relatively narrower in the outer rows in **paradoxus.* Also, the lower teeth differ in number from species to species, there being 9 series in **centrina* (6 specimens counted) contrasted with 13 in the type specimen of **paradoxus,* as Dr. Frade writes us, and 13 (perhaps 15) in the one specimen of the latter that we

have examined (counting is difficult). Rey (1928, Fig. 156, p. 470), it is true, credits **centrina* with 15, and pictures it thus. But this was prior to the discovery of the species **paradoxus*. There are 13 series of lower teeth in the specimen of **bruniensis* we have at hand.

Key to Species of *Oxynotus*

1. First dorsal fin spine sloping a little rearward; distance from tip of second dorsal spine to apex of second dorsal fin is about 1½ times as long as the spine, tip to base ..... **paradoxus* Frade 1929
   Eastern North Atlantic, known off the coasts of Morocco and of Ireland, and from the Gulf of Gascony. For records of occurrence, see Krefft 1955 and Tucker and Palmer 1949.

   First dorsal fin spine sloping forward; distance from tip of second dorsal spine to apex of second dorsal fin is not longer than the spine, tip to base 2
2. Interspace between first and second dorsal fins is at least 1½ times as long as base of second dorsal; distance from tip of first dorsal fin spine to apex of first dorsal fin is only ½-⅔ as long as the spine, tip to base; most, at least, of the dermal denticles on the sides with 3 cusps only ..... **centrina* (Linnaeus) 1758
   Eastern North Atlantic, including the Mediterranean.

   Interspace between first and second dorsal fins little if any longer than base of second fin; distance from tip of first dorsal spine to apex of first dorsal fin is a little longer than the spine, tip to base; most, at least, of the dermal denticles on sides with 5 cusps ..... **bruniensis* (Ogilby) 1893.
   Australia, Tasmania, New Zealand.

Family SQUALIDAE

First dorsal fin, like the second dorsal, with a series of radial supporting cartilages (Fig. 2, A, B); the trunk subcircular in cross section in most (for an exception see under *Cirrhigaleus*, p. 37); upper teeth as well as the lowers in several rows paralleling the jaw, with about as many teeth in any one row as in any other; dermal denticles with one central cusp (if any) in

most, with several cusps in some (p. 18); preoral clefts present in some, but lacking in others; see discussion, p. 12.

Key to Subfamilies of Squalidae

1. Each of the dorsal fins has a spine; preoral clefts present in all known genera, see discussion, p. 12; lips smooth ..... Subfamily Squalinae,[4] p. 18
   No spine in the second dorsal fin or in the first in most cases; preoral clefts lacking in most genera but present in some (see discussion, p. 12) 2
2. Teeth with only one cusp, the lowers much broader than the uppers; lips crenulate or smooth; dermal denticles with only one cusp or spine (if any) ..... Subfamily Dalatiinae, p. 109
   Teeth with several cusps, the uppers similar in shape to the lowers; dermal denticles often with two or more cusps or spines; lips smooth .. Subfamily Echinorhininae, p. 134

Subfamily SQUALINAE

Characters. Squalidae with a spine in each of the dorsal fins; the caudal axis raised, and the caudal fin wider below axis than above; longtitudinal dermal ridges, if any, confined to tail sector, posterior to level of cloaca; preoral clefts present in all known genera.

Remarks. Fowler (1934, p. 239; 1941, p. 223) restricted the subfamily Squalinae to those Squalidae in which the fin spines are not laterally grooved, and in which the caudal fin does not have a subterminal notch, to include *Squalus* Linnaeus 1758, and the barbel-bearing *Cirrhigaleus* Tanaka 1912. For those with laterally grooved fin spines and caudal fin with subterminal notch, he proposed Etmopterinae to include all the other known members of the group. But this scheme results in the union (as Etmopterinae) of species in which the upper teeth have at least three cusps (the lowers also in some) with other species in which the uppers, like the lowers, have only one cusp, a dental difference

[4] Previous to 1896 the sharks in question had commonly been referred to as Spinacidae or as Spinaces; e.g., by Müller and Henle 1841, by Bocage and Capello 1866, by Dumeril 1865, by Day 1880-1884, by Moreau 1881, and by Smitt 1895. The "Centrophoroidei" of Bleeker 1860 was an equivalent. The substitution of Squalidae by Jordan and Evermann 1896 doubtless stemmed from their realization that the generic name *Spinax* Cuvier 1817 was not available as the basis for the name of a family because it is a synonym of *Etmopterus* Rafinesque 1810.

that would seem as sound a basis for subdivision as is the nature of the fin-spines. And the use of the shape of the terminal part of the caudal fin as a primary character here seems forbidden by the differences in this respect among the species which (by their dentition) fall within the genera *Centroscymnus* and *Scymnodon*.

Genera. The members of the subfamily Squalinae as here defined fall in three divisions, as follows:

Division A — Fin spines without lateral grooves; lower contour of caudal fin without subterminal notch; teeth with only one cusp, the cusps of the uppers as well as of the lowers so strongly oblique as to form a nearly unbroken cutting edge along the jaw; the median tooth in each jaw basally overlapping the tooth next to it on either side, and the base of each succeeding tooth overlapping that of the next tooth outward along the jaw. This division includes the genera *Squalus* Linnaeus 1758 and *Cirrhigaleus* Tanaka 1912.

Division B — Fin spines with lateral grooves; lower contour of caudal fin with subterminal notch; upper teeth with three or more cusps, not overlapping basally, the lowers similar to the uppers in some (*Centroscyllium*), but with only one cusp in others (*Etmopterus*), and overlapping basally as in division A. This division includes two well-marked genera: *Centroscyllium* Müller and Henle 1841 and *Etmopterus* Rafinesque 1810.

Division C — Fin spines with lateral grooves and lower contour of caudal with subterminal notch (at least in most cases) as in division B; but teeth (uppers as well as lowers) with only one cusp; the uppers narrower than the lowers in most, either loosely spaced or with their bases in contact or slightly overlapping, the lowers broad based, with each tooth overlapping the next outward along the jaw as in division A. This group includes all known members of the subfamily other than those listed above for divisions A and B.

Students of sharks are now in general agreement as to the alternative characters of the genera *Squalus, Cirrhigaleus* (if the latter be accepted as distinct from *Squalus* — see p. 37), *Etmopterus* and *Centroscyllium;* i. e., divisions A and B. But the picture is not yet clear for the members of division C, which are deep-water species, few specimens of which have found their way into museum collections.

The members of division C that were set apart the earliest from the old genus *Squalus* Linnaeus 1758 were **S. squamosus* Bonnaterre 1788, and **S. granulosus* Bloch and Schneider 1801, both of which were transferred by Blainville (1816, p. 121) to his new genus *Acanthorhinus,* while *squamosus* was referred almost simultaneously by Cuvier (1817, p. 130, footnote 3) to his *Centrina.* But the earliest genus that was based in so many words on a member of this division was *Centrophorus,* proposed by Müller and Henle in 1837, for **C. granulosus* Müller and Henle, which they considered identical with **Squalus granulosus* Bloch and Schneider 1801. And their subsequent description and illustration of it (Müller and Henle 1841, p. 89, Pl. 33) were so satisfactory that there is no doubt as to the specific identity of the Mediterranean specimen which they had at hand.

A year later Bonaparte (1838, p. 207; 1839, p. 9, extra) proposed the generic name *Lepidorhinus* for **squamosus,* while Lowe in 1839 instituted *Acanthidium* for two Madeiran species, one of which (**calceum* Lowe 1839) falls in the group with which we are dealing, whereas the other (*pusillum* Lowe 1839) is now known to be an *Etmopterus* (p. 49).

Next, Gill (1862, pp. 496, 498) made the **Squalus uyato* of Rafinesque 1810 the basis of a new genus, *Entoxychirus,* setting it off from the old genus *Squalus* by its fins, from *Centrophorus* Müller and Henle 1837 under the misconception that the teeth of **uyato* are equally oblique in both jaws. This error was no doubt based on an illustration that Bonaparte (1841, Pl. 57, fig. 2) credited to **uyato,* but which actually pictured the teeth of a *Squalus,* as Garman (1913, p. 198) has pointed out. The relegation of *Entoxychirus* to the synonymy of *Centrophorus* by Garman (1913, p. 196), but its revival by Fowler (1941, p. 242) for species with "pectoral angle extended," contrasted with "not or scarcely extended" in *Centrophorus,* covers the subsequent history of the genus.

In 1864, Bocage and Capello proposed two new genera for members of the division in question: *Centroscymnus,* type species **C. coelolepis* Bocage and Capello 1864, and *Scymnodon,* type species **S. ringens* Bocage and Capello 1864, based in each case on a newly discovered shark from deep water off Portugal. These species were described by them in greater detail, with excellent illustrations two years later (Bocage and Capello 1866, pp. 30,

32, Pl. 1, fig. 1, Pl. 2, fig. 3, Pl. 3, figs, 2a 2b). And while Günther (1870, p. 420) did not regard the dental differences on which these two genera were based as sufficient to separate them from *Centrophorus*, Garman (1906, p. 204) and Regan (1908, p. 39) revived them, Garman without stating his reasons, but Regan because of the same dental characters on which Bocage and Capello had set them up originally.

Meantime, Johnson, in 1867, had proposed the genus *Machephilus* for his new Madeiran species *dumerili*, separating it from *Centrophorus* because of the presence of a symmetrical median tooth in its lower jaw. However, subsequent authors (Garman 1913, p. 212; Rey 1928, p. 440; Bigelow, Schroeder and Springer 1953, p. 224) have classed *dumerili* as a synonym of **Centrophorus squamosus* (Bonnaterre) 1788, i.e., have not considered the presence or absence of a symmetrical median lower tooth as sufficient ground for generic separation, and this same course is followed here (p. 72).

The next landmark in the taxonomic history of the squaline sharks of division C was the institution by Jordan and Snyder in 1902 of the genus *Deania*, type species **eglantina* Jordan and Snyder, a Japanese shark characterized by a very long snout as well as by pitchfork-shaped denticles on the sides of its trunk. And this generic entity was accepted by Garman (1906, p. 205; 1913, p. 215). But Garman's revival of the generic name *Acanthidium* Lowe 1839 for it, in place of *Deania*, was not well judged, for the type species of *Acanthidium* (**pusillum* Lowe 1839) as designated by Goode and Bean (1895, p. 10), by Jordan and Evermann (1896, p. 55), and by Jordan (1919, p. 195) falls within the limits commonly accepted for the genus *Etmopterus* Rafinesque 1810. Consequently, Fowler's (1941, p. 237) relegation of *Acanthidium* to the synonymy of *Etmopterus* is to be accepted — unless indeed Whitley's (1939, p. 266) separation of *Acanthidium*, type species *Centrina nigra* Lowe 1834 (**Acanthiduim pusillum* Lowe 1839[5]) from *Etmopterus* Rafinesque 1810, type species **Squalus spinax* Linnaeus 1758, is to be followed. And the grounds stated by Whitley (i.e. *Acanthidium* with "first dorsal much smaller than the second and the ventrals just before the level of the first dorsal") do not seem to justify

[5] Whitley (1939, p. 266) points out that it was as *Centrina nigra* that Lowe (1834, p. 144) first reported the shark which he renamed **Acanthidium pusillum* in 1839.

generic division in this case, for the relationship in size between the first and second dorsals is about the same among our Norwegian and Mediterranean specimens of **spinax* (type species of *Etmopterus*) as it is in the type species of Lowe's (1839) genus *Acanthidium*. Also, the rear end of the bases of the pelvics ranges in position from below the second dorsal spine to considerably anterior to the latter among the several Atlantic species of *Etmopterus* (Bigelow, Schroeder and Springer 1953, p. 272).

A year after the genus *Deania* had been proposed by Jordan and Snyder (1902), Jordan and Fowler (1903, p. 633) made the Japanese *Centrophorus squamulosus* Günther 1877 the type of still another genus, *Zameus*, separating it from *Centrophorus* by the shape of its dermal denticles. And while Garman (1913, p. 207) classed *Zameus* unequivocally as a synonym of *Scymnodon* Bocage and Capello 1864, Fowler (1941, p. 226) has revived it as a subgenus of the latter, now invoking the length of the orbit as compared with the length of the snout as the alternative subgeneric character.

Next Smith and Radcliffe (1912, p. 681) made their new Philippine species **profundorum* the type of another new genus, *Nasisqualus*, but without mentioning anything to separate it from *Deania* Jordan and Snyder 1902, with which Regan (1912) has synonomized it. And during the following year Garman (1913, p. 206) proposed *Centroselachus* for the Portuguese shark that Bocage and Capello (1864, 1866) had originally described and pictured as **Centrophorus crepidater*, basing its generic separation from *Centrophorus* Bocage and Capello 1864, and from *Scymnodon* Bocage and Capello 1864 on small differences in the shapes of the dermal denticles. Garman (1913, pp. 189, 211) also revived the genus *Lepidorhinus* Bonaparte 1838, type species **Squalus squamosus* Bonnaterre 1788, but this revival has not been accepted generally.

Nine years after the appearance of Garman's monograph, Gilchrist (1922, p. 48, Pl. 7, fig. 3) proposed the genus *Atractophorus* for a southern African squalid, *A. armatus* Gilchrist, in which the tip of the second dorsal fin spine is described as barbed, like an arrowhead (p. 82). Next Whitley (1932, p. 326) proposed *Deaniops*, with the Australian *Acanthidium quadrispinosum* McCulloch 1915 as type, without including any generic diagnosis at the time, but adding subsequently (Whitley 1939,

p. 266) that it was for "species with a long low first dorsal fin." Two years later Fowler (1934, p. 293) proposed *Proscymnodon*, type species *Centrophorus plunketi* Waite 1909, from New Zealand, as a subgenus of *Scymnodon,* because of length of orbit combined with the positions of the first and second dorsal fins, and *Proscymnodon* has been accepted by Whitley (1934, p. 199; 1940, p. 142) as a full genus. Whitley (1940, pp. 145, 146) subsequently has proposed two subgenera within the old genus *Centrophorus* Müller and Henle 1837, *Gaboa* (type species *Centrophorus harrisonii* McCulloch 1915, Australia) and *Somnispinax* (type species *Centrophorus nilsoni* Thompson 1930, also from Australia), the former because of "the form of its teeth and denticles," the latter because of smooth edged teeth, "differently shaped denticles, differently shaped snout, fins, etc.," but without more precisely specifying what these differences are. As a final complication, Fowler's (1941, p. 223) definition of *Entoxychirus* as with "inner pectoral angles extended" corresponds to Garman's (1913, p. 189) for *Centrophorus,* while Fowler's for *Centrophorus* ("pectoral angles not or scarcely extended") corresponds to Garman's for *Lepidorhinus.*

To sum up, such of the Squalinae as have grooved fin spines, upper teeth as well as the lowers with only one cusp, and caudal fin with a subterminal notch, have been referred to 18 different genera or subgenera at one time or another. But our own study of a broad representation of the group leads us to conclude that the genera *Centrophorus* Müller and Henle 1837, *Centroscymnus* Bocage and Capello 1864, *Scymnodon* Bocage and Capello 1864, and *Deania* Jordan and Snyder 1902, perhaps with the addition of *Atractophorus* Gilchrist 1922, afford appropriate resting places for all of them — provided that a genus, to be of practical value, must be "separated from other similar units by a decided gap" (Mayr, Linsley and Usinger, 1953, p. 48). And we may add that we subscribe heartily to this proviso.

The characters that have proved the most useful, here, for the definition of genera (because they are the most definitely alternative between groups of species) are: the shapes of the teeth, the shape of the inner corner of the pectoral fins, the relative length of the snout, the length of the exposed portion of the second dorsal fin spine, and perhaps also whether the tip of that spine is smooth or is barbed or otherwise expanded, as it is described

for one member of the group (p. 82). The differences in relative size, and in length at base, of the first and second dorsal fins (sometimes invoked as of generic significance) are not sharply alternative enough to be of much help in this regard. And recent discoveries (p. 87) have also proved that the shape of the dermal denticles on the sides of the trunk is not as reliable a generic criterion here as we had formerly believed. For further details in this last regard, see our earlier discussion (Bigelow and Schroeder 1954, p. 47), to which we should add that as early as 1861 Steenstrup had already pointed out that the dermal denticles of sharks do not persist throughout the life of the individual, as the scales of bony fishes do, but are short lived, to be replaced as they are shed by more newly formed denticles.

Synopsis of Genera of Squalinae

1. Upper teeth as well as the lowers with one cusp only 2
   Upper teeth with 3-7 cusps 7
2. Fin spines well developed, without lateral grooves, caudal fin without subterminal notch, its tip not truncate; upper teeth similar in shape to lowers 3
   Fin spines with lateral grooves; lower margin of caudal fin with a definitely outlined subterminal notch and with its tip more or less truncate, at least in most species; upper teeth differing more or less widely in shape from the lowers, except as noted on pages 26 and 38 4
3. Anterior margin of nostril does not bear a barbel; caudal peduncle with a longitudinal ridge along either side, and with a precaudal pit above but none below; upper teeth, like the lowers, with the successive cusps directed outward strongly along either side of the jaw .....
   Squalus Linnaeus 1758, p. 26
   Anterior margin of nostril with a conspicuous barbel reaching beyond the mouth; caudal peduncle without longitudinal ridges and without precaudal pit; other characters, in general, including teeth, as in *Squalus* ..... *Cirrhigaleus* Tanaka 1912, p. 37
4. Inner corner of pectoral fins angular and more or less extended (see discussion, p. 66); fin spines well developed, the second longer than the first; upper teeth narrower than the lowers and more nearly erect in most cases; lowers directed strongly outward; cutting edge of lower teeth smooth in some but more or less irregularly and finely serrate in others (p. 67, Fig. 9); snout in front of mouth not longer than from mouth to level of origin of pectoral fins; dermal denticles on

sides of body low, block-like, scale-like, or conical .....
Centrophorus Müller and Henle 1837, p. 63
Inner corner of pectoral fins not extended; rounded in most, perhaps quadrate in one known species 5

5. Upper teeth midway along either side of the jaw noticeably longer than those toward center of the mouth (Fig. 13C); first and second dorsal fin spines projecting only slightly beyond the skin; dermal denticles on sides of body low, scale-like, with tridentate rear margin; other characters in general as in *Centroscymnus* (alternative 6; see also p. 85) ..... *Scymnodon* Bocage and Capello 1864. p. 96
Upper teeth midway along either side of jaw only slightly longer than those toward center of mouth (Fig. 12C) 6

6. Snout in front of mouth not longer than from mouth to level of origin of pectoral fins; inner corner of pectoral fins broadly rounded; dorsal fin spines either exposed at the tip or entirely enclosed in the skin; lower teeth smooth-edged, the cusps directed strongly outward; upper teeth lancet-shaped, much narrower than lowers, and more nearly erect; dermal denticles on sides of body scale-like, tridentate or evenly rounded, low in adults of known species but rising more steeply from skin on juveniles of at least one (p. 90); subterminal notch of caudal fin well marked in most species, but indistinct in juveniles of one named species, the parentage of which is not yet definitely known (p. 94) ..... *Centroscymnus* Bocage and Capello, 1864. p. 84
Snout in front of mouth longer than from mouth to level of origin of pectoral fins; inner corner of pectoral fins rounded in most, perhaps quadrate in one of known species (p. 102), but not extended at all; both of the dorsal fin spines well exposed; caudal fin with well marked subterminal notch; teeth smooth edged; the uppers narrow, triangular, on broad bases; the lowers strongly oblique in the females of all known species, but less so in the males of some (p. 103); dermal denticles on sides of body pitchfork shaped, rising steeply from the skin; other characters in general as in *Centrophorus* (p. 63) .....
Deania Jordan and Snyder 1902, p. 101

7. Lower teeth with 3-5 cusps and similar to the uppers in shape; dorsal fin spines well developed, with lateral grooves; caudal fin truncate and with subterminal notch in known species (but see discussion, p. 46); caudal pedunele without precaudal pits or lateral longitudinal ridges; dermal denticles on sides of body slender, thorn-like .....
Centroscyllium Müller and Henle 1837, p. 38
Lower teeth with only one cusp, much wider than uppers; dermal denticles on sides of body bristle- or conical thorn-like to truncate; other characters in general as in *Centroscyllium* .....
Etmopterus Rafinesque 1810. p. 47

Genus SQUALUS Linnaeus 1758

Squalus Linnaeus 1758, p. 233, type species **S. acanthias* Linnaeus, designated by Gill, 1861, p. 369.

For generic synonyms, see Bigelow and Schroeder, p. 452.

Generic characters. Squalinae with fin spines well developed, without lateral grooves; caudal fin without subterminal notch but with well marked lower-anterior lobe; caudal peduncle with a longitudinal ridge along either side, and with a pre-caudal pit above but none below; margin of nostril without barbel; preoral clefts present, slightly expanded inwardly; snout in front of mouth considerably shorter than from front of mouth to origin of pectorals; inner corner of pectoral fins either rounded, subangular, or slightly extended; dermal denticles lanceolate, heart-shaped, or tridentate with sharp tip, and of different shapes on different parts of the trunk as well as from species to species; teeth in both jaws with only one cusp, directed so strongly outward as to form a practically unbroken cutting edge along either half of the jaw; the base of each tooth overlapping that of the next tooth, outward. Maximum length a little more than one meter.

Depth range. The depth range recorded for this genus is from the surface down to about 380 meters. Thus **S. acanthias* (p. 30) occurs in numbers anywhere between the surface and the 160-180 meter level. **S. fernandinus* ranges from close to the surface (reported at 16-20 meters by Poll, 1951, p. 62) down to the maximum depth reported above for its genus, while the center of abundance lies considerably deeper for it than for **acanthias*, to judge from Poll's (1951, p. 61) report of 608 specimens trawled at 220 meters off equatorial West Africa. And it seems that neither **cubensis* (reported from 137-384 meters) nor **megalops* rise, normally, as near to the surface as does **acanthias* or **fernandinus*.

Species. All known representatives of the genus *Squalus* from various parts of the world (under whatever names they may have been reported) seem referable to one or other of three divisions as defined by the shape of the pectoral fins; by the position (farther forward or rearward) of the first dorsal fin; by the presence or absence of a small secondary lobelet on the outer edge of the flap-like expansion of the anterior margin of the nostril;

and by the color pattern. In the following discussion each of these divisions is referred to under the name of its earliest described representative.

The differences in the shape of the pectorals, as outlined below, are so obvious that no further discussion of them is called for just here. Similarly, the position of the first dorsal spine, relative to that of the origin of the pectoral fins, has proved definitely alternative for the specimens yet measured, though with the reservation that measurements of a larger number may eventually narrow the gap in this respect. And the shape of the narial flap seems equally diagnostic for the majority of specimens, though we have seen one individual of the *fernandinus* division where one of the nostrils shows the secondary lobelet, but the other does not — a situation analogous to that of the shape of the inner corner of the pectoral fins in *Centrophorus* (p. 67). But our earlier selection (Bigelow and Schroeder 1948, p. 455; Bigelow, Schroeder and Springer 1953, p. 221) of the midpoint of the bases of the pelvics relative to the positions of the dorsals as a species-criterion was a less happy one, for additional information has shown that in this respect the extremes intergrade. And while the presence of white spots is diagnostic for the specimens that show them, the absence of white markings is not diagnostic, for it has long been known that in the type species of the genus (*acanthias*) these spots tend to fade with growth, while some large specimens show no trace of them.

Synopsis of divisions of *Squalus*

Acanthias division. Inner corner of pectoral fins well rounded: the distal margin not deeply concave; point of emergence from skin of 1st dorsal spine is posterior to 5th gill openings by a distance as long as from anterior margin of eye to 5th gill openings or slightly longer; midpoint of base of pelvics about midway between a perpendicular at point of emergence of 2nd dorsal spine and one at free rear tip of 1st dorsal on most specimens, but nearer to tip of 1st dorsal than to 2nd dorsal spine on one large male from Massachusetts (Mus. Comp. Zool. No. 35863) that we have seen. Anterior narial flap simple, without secondary lobelet on its outer edge. Sides of trunk marked with white spots on small and middle sized specimens, more faintly so on larger ones.

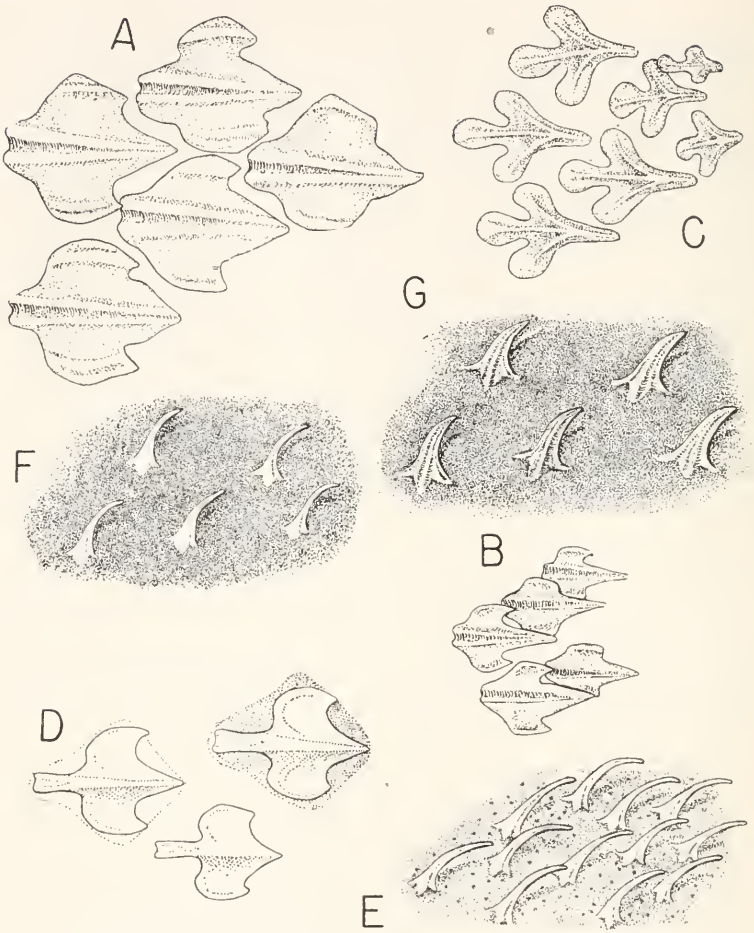

Fig. 3. Dermal denticles from side of body below first dorsal fin. A, *Squalus fernandinus*, female, 914 mm. long, island of Juan Fernandez, Mus. Comp. Zool. No. 841, x about 50. B, *S. fernandinus*, male, 397 mm. long, off South Carolina, Mus. Comp. Zool. No. 37064, x about 50. C, *S. megalops*, same specimen as in Fig. 4A, x about 70. D, *Squalus acanthias*, Massachusetts, x about 34, after Bigelow and Schroeder 1948, Fig. 88C. E, *Etmopterus spinax*, female, 250 mm. long, Norway, Mus. Comp. Zool. No. 1022, x about 15. F, *Etmopterus princeps*, female, 165 mm. long, offing of Nantucket, Mus. Comp. Zool. No. 37403, x about 12. G, *Etmopterus princeps*, female, 610 mm. long, offing of southern edge of Georges Bank, Mus. Comp. Zool. No. 37445, x about 10.

while some adults lack these spots altogether. Dermal denticles on sides below 1st dorsal fin of the shape shown in Figure 3D.

Fernandinus division. Inner corner of pectorals about a right angle, more or less blunted, the distal margin weakly concave; point of emergence from skin of 1st dorsal spine is posterior to 5th gill openings by a distance at least not longer than from anterior edge of eye to 2nd gill openings, and slightly shorter than that in most; midpoint of base of pelvics at least as near to a perpendicular at rear tip of 1st dorsal as to one at emergence from

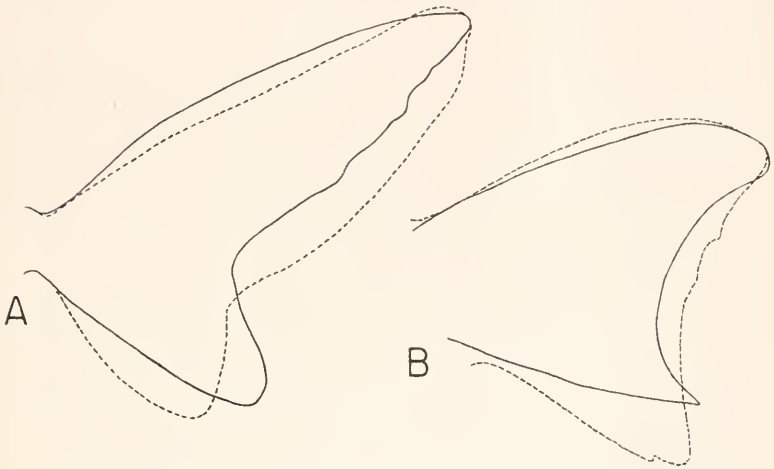

Fig. 4. Outlines of fins of *Squalus megalops* and of *Squalus cubensis*, superimposed to show the differences in shape. A, caudal fins of *S. megalops*, female 526 mm. long, New South Wales, Mus. Comp. Zool. No. 38619 (dotted line), and of *S. cubensis*, female, 672 mm. long, Cuba, Mus. Comp. Zool. No. 1461 (solid line), adjusted to equal lengths along upper margin. B, pectoral fins of *S. megalops* (type specimen), from drawing kindly contributed by Dr. G. P. Whitley (dotted line), and of *S. cubensis*, same specimen as in A (solid line), adjusted to equal lengths along outer margin.

skin of 2nd dorsal spine, and nearer on most (but see above, under *acanthias* division); anterior narial flap with a small secondary lobelet on its outer edge (Bigelow and Schroeder 1948, Fig. 87F), though in occasional specimens this lobelet may be lacking on the one nostril or on the other (see above); dermal denticles on sides below first dorsal fin simpler in form than in

acanthias division, tridentate, the marginal points longer on the denticles of small specimens than on those of larger (Fig. 3, A, B). Trunk without white markings at any stage in growth.

Megalops division. Inner corner of pectoral fin pointed, or only very slightly blunted, the distal margin deeply concave (Fig. 4B); relative positions of fins, shape of narial flap, and color (without spots) essentially as in *fernandinus* division (see above); dermal denticles on sides below first dorsal fin differing from those both of the *acanthias* division and of the *fernandinus* division in a way easier presented pictorially (Fig. 3C) than verbally.

Remarks. There is no danger of confusing any representative of the *megalops* division with any of the *acanthias* division or any of the *fernandinus* division, so sharply diagnostic is the shape of the pectoral fins. But the discontinuity as regards fin characters is so small between the *acanthias* and the *fernandinus* divisions that identification as the one or the other of large plain-colored specimens may call for close scrutiny of the shape of the narial flap and of the denticles.

Acanthias division. **Squalus acanthias* Linnaeus 1758, type species of the genus[6] and locally the most numerous of sharks, represents this division in the North Atlantic, where its regular range extends in the east from Iceland, Norway and the Murman coast to Morocco (including the Mediterranean and the Black Sea), with reports from the Canaries and Senegal; and in the west from southeastern Labrador (straying to southwest Greenland) to the southern part of the North Carolina coast in abundance, with a few ranging to southern Florida and to Cuba.[7]

The common spiny dogfish of the coast of the northwestern Pacific was originally described as a separate species, **suckleyi* Girard 1854, and it has most often been reported under that name. But our own comparison of Californian specimens with others from both sides of the North Atlantic has not revealed any consistent differences that might be regarded as specific, whether in the position of the first dorsal fin relative to the pectorals (the character the most often invoked as alternative), or in any other respect (Bigelow and Schroeder 1948, p. 453).

[6] For synonyms see Bigelow and Schroeder 1948, p. 467.

[7] For details, see Bigelow and Schroeder 1948, pp. 463-464.

Spiny dogfishes of the *acanthias* division have been reported from northeastern Asia both as **acanthias* Linnaeus 1758 and as **suckleyi* Girard 1854; from Japanese waters under the name *vulgaris* Risso 1826, repeatedly as **suckleyi* Girard 1854, as *mitsukurii* Jordan and Fowler 1903 (their illustration, but not their description, which was based on an example of the *fernandinus* division, see below, p. 33), and as *wakiyae* Tanaka 1918, a name proposed by Tanaka for the shark that had been pictured by Jordan and Fowler (1903, p. 630, fig. 3) as *mitsukurii;* from Korea, China and Formosa as *suckleyi.* There is nothing, however, in available information to suggest that these populations differ specifically, one from another, or from the typical **acanthias* of the North Atlantic. Schmidt (1931, p. 7) indeed, has long since expressed a doubt as to whether the spiny dogfishes of the *acanthias* division of Japan are separable from those of the Black Sea. For North Pacific references to *Squalus* of the *acanthias* division, see Bigelow and Schroeder 1948, p. 472.

A representative of the *acanthias* division has also been credited (by name only) to Hawaii (Fowler 1930, p. 495, as *S. suckleyi*). But an earlier report of *mitsukurii* from Hawaiian waters proves actually to have been based on **S. fernandinus* (p. 33).

The *acanthias* division has not been reliably reported for the equatorial-subequatorial belt, whether of the Atlantic or of the Indo-Pacific. But seemingly it is as widespread in mid-latitudes of the southern hemisphere as it is of the northern. Thus sharks apparently of this division have been reported from southern Africa as **acanthias* and as *vulgaris*; from Uruguay and northern Argentina as **acanthias;* from the Magellanic region as **acanthias* and as *lebruni* Vaillant 1888[a]; from Chile as **suckleyi* (by Fowler 1930, p. 495); from New Zealand as **fernandinus* (by Waite 1909, p. 142, Pl. 16, fig. 1) but identity as *acanthias*-like established by rearward position of first dorsal fin and by white spotted sides, and as *kirki* Phillipps 1931; from Australia as *vulgaris* (repeatedly) and as *whitleyi* Phillipps 1931 (see also Whitley 1940, p. 193); and from the island of Reunion in the southern Indian Ocean as *vulgaris.* No one of these southern populations, however, has yet been studied in detail, nor has anything developed within the past few years to contradict our

earlier statement (Bigelow and Schroeder 1948, p. 454) that "the relationship of these southern hemisphere forms to one another and to the northern *acanthias* is uncertain."

Fernandinus division. The earliest named representative of this division is *Squalus fernandinus* Molina 1782, originally described from the island of Juan Fernandez off the coast of Chile. And our recent comparison of a female, 520 mm. long (Mus. Comp. Zool. No. 446) from Nice, France, with a **fernandinus* of 914 mm. from the type locality, as well as with others from the Gulf of Mexico and from the offing of South Carolina, has confirmed the conclusion earlier arrived at by Garman (1913, p. 195), by Poll (1951, p. 59), and by Bigelow, Schroeder and Springer (1953, p. 222), that the shark described from the Mediterranean in 1826 by Risso under the species-name *blainvillii* (Risso 1826, p. 133, Pl. 3, fig. 6) is identical with *fernandinus*. This joint species (most often reported as "*blainvillii*") occurs widespread in the Mediterranean, in the Black Sea, and off the open Atlantic coast from Portugal southward to equatorial waters (reported from 6° 31′ S., see Poll 1951, p. 59). And it is to be expected all along the West African seaboard to the southward, for spiny dogfishes apparently identical with **fernandinus* have been reported in abundance in southern African waters, both as *blainvillii* (by Bleeker, 1860, pp. 50, 58, 80, and by Günther 1870, p. 419): as *acutipinnis* Regan 1908 (by Regan 1908[a], p. 248, and by Barnard 1925, p. 48), and as **fernandinus* (by Gilchrist 1922, p. 48, by von Bonde 1924, p. 5, and by Smith 1949, p. 60). **S. fernandinus* is known in the western side of the Atlantic also, both from the offing of South Carolina and in the Gulf of Mexico in the north (Bigelow, Schroeder and Springer 1953, p. 220), and off the coast of Argentina in the south (for locality records from the western South Atlantic, see Bigelow and Schroeder 1948, p. 480). But the number of specimens so far reported from the western side of the Atlantic, north or south, has not been large enough to suggest that **fernandinus* is as plentiful there, or as generally distributed, as it is in the eastern side, and in the Mediterranean.

The reports that have come to hand for **fernandinus* in the Indo-Pacific are numerous enough, and are distributed widely enough to show that it is as widespread there as it is in the Atlantic, not only in the temperate zones both north and south but

in tropical-subtropical latitudes as well. Thus **fernandinus,* or a form so closely allied to it that no significant differences appear from the published accounts, is widespread in Japanese waters, whence it has been reported as *mitsukurii* Jordan and Fowler 1903 (their description, but not their illustration, which was based on a specimen of the *acanthias* division, see above p. 31[8]); repeatedly also as *japonicus* Tanaka 1917 (for an excellent description and illustration, see Tanaka 1917, p. 467, Pl. 30, figs. 366, 367). It has also been described and pictured from southern China by Fang and Wang (1932, pp. 249, 250, fig. 16), not only under the name *mitsukurii* Jordan and Fowler 1903, but also as *brevirostris* Tanaka 1917, though this last name had actually been based on the Japanese representatives of the *megalops* division, not on one of the *fernandinus* division (see below, p. 36).

The specific identity of the spiny dogfishes that had been reported by Snyder (1904, p. 515), by Jordan and Evermann (1905, p. 45), by Gilbert (1905, p. 580), and by Günther (1910, p. 490), from the Hawaiian Islands under the name *mitsukurii* Jordan and Fowler 1903, had remained uncertain, for the brief descriptions seemed equally applicable to the *fernandinus* division of the genus or to the *megalops* division. But our recent examination of five of Jordan and Evermann's and Gilbert's specimens has shown nothing to separate them specifically from the specimens of **fernandinus* which we have seen from the offing of South Carolina, from the Gulf of Mexico, from the Mediterranean, and from Juan Fernandez (type locality), whether in relative positions of fins, in bodily proportions, or in the shape of the denticles on the sides of the body.

**S. fernandinus* has also been reported from the Philippines under its own name (with brief description) by Herre (1923, p. 73; 1934, p. 12); also as *philippinus* Smith and Radcliffe (1912, p. 677, Pl. 51, fig. 1), a supposedly new species based, however, on a specimen that is not separable from *fernandinus* either in fin characters or in its denticles, as Mr. Stewart Springer informs us from a recent examination of it in the U. S. National Museum. We should note in passing that Whitley (1931, p. 310) had proposed a new name, *montalbani,* to replace *philippinus* Smith and Radcliffe, the latter name having long been preoccupied within

[8] On this point, see also Jordan and Hubbs 1925, pp. 105-106.

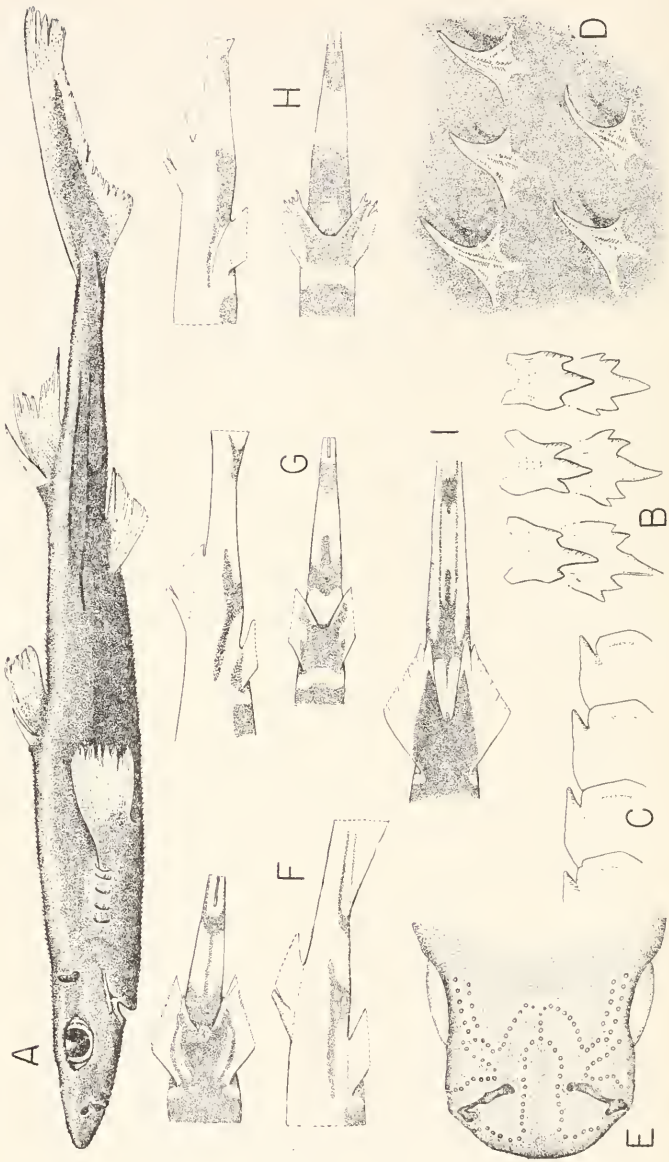

FIGURE 5

the genus *Squalus* by *philippinus* Shaw 1804 (p. 341), proposed for an Australian heterodontid. For details see Whitley.

**S. fernandinus,* to continue, has been reported from Mauritius, both as *blainvillei* (by Sauvage 1891, p. 11) and as *acutipinnis* (by Regan 1908, p. 47). It has long been known also in Australian waters, where it seems first to have been reported, with at least presumptive evidence of identity, by Günther (1870, p. 419) as *blainvillei,* and subsequently by that same name but without description by MacLeay (1881), by Ogilby (1889, p. 185), and by Lucas (1890, p. 44). A confusing feature here is that the only Australian report of a spiny dogfish under the name **fernandinus,* the identification of which was supported by a description or by an illustration (Waite 1921, p. 23, fig. 30), seems not to have been based on that species, but on the local representative of the *megalops* division of the genus.

Regan's (1908, p. 46) identification, however, of a spiny dogfish from Tasmania as **fernandinus* was no doubt correct, for we have found nothing to separate the type specimen of **tasmaniensis* Rivero 1936 (now in the Museum of Comparative Zoology) from our specimen of **fernandinus* from the type locality of the species (Juan Fernandez). For an extensive list of Indo-Pacific records for *fernandinus* see Herre 1953, p. 31.

With the evidence of widespread occurrence so conclusive for *fernandinus* for the Australian region in general, it seems astonishing that there has been no report yet for New Zealand waters of a spiny dogfish, the accompanying account of which places it definitely in **fernandinus.* In fact, the only report under that name of a New Zealand *Squalus* that includes any clear evi-

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Fig. 5, A, *Etmopterus bullisi,* new species, juvenile male, 230 mm. long (U. S. Nat. Mus. No. 158186), off northeastern Florida. B, upper teeth of same, x about 9. C, lower teeth of same x about 12. D, dermal denticles of same, from side below first dorsal fin, x about 30. E, *Etmopterus polli,* immature male about 226 mm. long, off south equatorial West Africa, Mus. Comp. Zool. No. 38000, lower surface of anterior part of head, x about 1.4. F, *Etmopterus spinax,* Norway, to show black pattern on posterior part of trunk. G, corresponding drawings of *E. virens,* northern part of Gulf of Mexico. H, corresponding drawings of *E. hillianus,* north coast of Cuba; F-H, x about 0.4, after Bigelow, Schroeder and Springer 1953, Fig. 6. I, corresponding drawing of *E. abernathyi,* type specimen, x about 0.4, after Garrick 1957, Fig. 3C.

dence of specific identity (Waite 1909, p. 142, Pl. 16, fig. 1; Phillipps 1928, p. 223, fig. 3) was evidently based on a member of the *acanthias* division. Thus the accompanying illustration shows its sides as white spotted, its first dorsal fin as originating posterior to the rear inner corner of the pectorals when the latter are laid back, and the mid-point of the bases of its pelvics as nearer to the origin of the second dorsal than to the rear end of the base of the first dorsal.

It is astonishing, also, that while **fernandinus* must be common around Juan Fernandez, to judge from the number of specimens that have found their way thence to various museums (Delfin 1901, p. 21), and is reported from northern Argentine waters, on the conclusive evidence of a small one found in the stomach of an albatross (Lahille 1928, p. 327, fig. 17), we have found no positive report of its presence in continental waters along the coast of Chile. Thus Philippi's (1887, p. 27) inclusion of it (under the name *firmandezianus*) in his account of the sharks of Chile seemingly harked back to Molina's original report of it from Juan Fernandez. Neither does Delfin (1901) mention any Chilean localities for it other than Juan Fernandez, which is some 240 miles off the Chilean coastline; nor does Fowler's (1930, p. 495) nominal reference of it to "Chile" include any continental locality. Neither has it been reported from Peru, nor from the Pacific coast of Central or North America, for that matter.

Megalops division. The earliest adequate account (with illustration) of a representative of this was by McCulloch (1927, p. 9, Pl. 2, fig. 25a; illustration later copied by Whitley 1940, p. 138, fig. 147) of an Australian shark that was identified by him as **megalops* MacLeay 1881. And Dr. Whitley writes us that he has verified this identification, by comparison with the type specimen of **megalops*, which he has had the kindness to examine at our request. The accompanying illustration (Fig. 4B) reproduces a tracing of its pectoral fin which Dr. Whitley has kindly sent us. We are also fortunate enough to have at hand three excellent specimens of **megalops*, 526-550 mm. long, from New South Wales, for which the Museum is indebted to Col. John K. Howard.

The Japanese *brevirostris*, described and beautifully pictured by Tanaka (1917, p. 464, Pl. 129, figs. 362, 363; Pl. 130, fig. 364)

resembles **melagops* so closely that we have no doubt a comparison of specimens from the two regions would lead to their union as **megalops,* this being the older of the two names.

The **megalops* division is represented in the Atlantic by **cubensis* Rivero 1936, which is known from Cuban waters (type region), from the northwestern part of the Gulf of Mexico, (specimen recently taken by "Oregon" and referred to us by Mr. Stewart Springer), probably Trinidad and from Rio de Janeiro, whence it was reported by Ribeiro (1907, p. 168) under the name *blainvillei* (Bigelow and Schroeder 1948, p. 478, footnote 63).

**S. cubensis* closely resembles **S. megalops* in proportional dimensions, and in the shape of the denticles on the sides of its body (Fig. 3), but differs in a relatively longer first dorsal fin spine, in somewhat differently shaped caudal and pectoral fins (Fig. 4), and in the location (relative to the dorsal fins) of the pelvic fins, the midpoint of the bases of which are about midway between the rear end of the base of the first dorsal and the origin of the second dorsal in **cubensis* (a little nearer to the rear end of the base of the first dorsal than to the origin of the second dorsal in **megalops*). No representative of this division of the genus has yet been reported from the eastern side of the Atlantic, or from the Mediterranean.

Genus CIRRHIGALEUS Tanaka 1912

Cirrhigaleus Tanaka 1912, type species *C. barbifer* Tanaka 1912b, p. 151, Pl. 41, figs. 156-162; Japan.

Generic synonym:

Phaenopogon Herre 1935, type species *P. barbulifer* Herre 1935, p. 123, fig. 1; Japan.

Generic characters. In general as in *Squalus* (p. 26), but without precaudal pit either above or below; posterior part of trunk without longitudinal ridges; and anterior margin of nostril, near inner end, with a well developed and very conspicuous fleshy barbel tapering to a slender tip (a feature unique among squaloid sharks); dermal denticles on sides of body with tridentate rear margins, their outer surface with three corresponding ridges. Also, in the only species that has yet been seen, the back is more highly arched than it is in any known *Squalus,* and

the body is subtriangular in cross section. Maximum recorded length 855 mm.

Remarks. Garman (1913, p. 457), followed by Fowler (1941, pp. 255, 275) reduced *Cirrhigaleus* to a subgenus of *Squalus* in rank. But the presence of the nasal barbel, combined with the lack of precaudal pits and of longitudinal-lateral ridges on the caudal peduncle seem fully to justify its retention as a distinct genus. *Phaenopogon* Herre, proposed without mention of Tanaka's (1912) earlier account of *Cirrhigaleus,* is clearly equivalent to the latter, to the synonymy of which Herre himself (1936, p. 59) has already relegated it.

Species. One species only is known, *C. barbifer* Tanaka 1912, which was based on a single male, 855 mm. long, from the Tokyo market. A second specimen (a female of 555 mm.) from Misaki, Japan, has more recently been described and pictured by Herre (1935, p. 123, fig. 1) as *Phaenopogon barbulifer.*

Genus CENTROSCYLLIUM Müller and Henle 1841

Centroscyllium Müller and Henle 1841, p. 191. Type species **Spinax fabricii* Reinhardt 1825, West Greenland.

Generic synonym:

Paracentroscyllium Alcock 1889, p. 379, type species *P. ornatum* Alcock, Bay of Bengal.

Generic characters. Squalinae with upper teeth similar to lowers, erect and symmetrical, or nearly so, all along the jaw; the teeth in both jaws with 3-5 cusps, the median cusp much the largest; dorsal fin spines well developed, with two longitudinal grooves on either side; lower posterior margin of caudal fin with subterminal notch (but see discussion, p. 46); caudal peduncle without precaudal notch either above or below, and without lateral-longitudinal ridges; inner corner of pectoral fins rounded in known species; snout in front of mouth not more than one-half as long as head to origin of pectoral fins; preoral clefts present, slightly expanded inwardly; dermal denticles thorn-like, on stellate bases; newborn specimens naked, the denticles developing first along the back, spreading later to sides, and subsequently to the lower surface (see further, p. 41); some species, at least, with thickenings of the skin that presumably are luminous. Maximum recorded length 829 mm., for *C. fabricii.*

Depth range. The only member of this genus for which we have more than scattered records (*fabricii,* p. 41) seldom (if ever) has been taken shoaler than 275 meters; its center of abundance lies deeper than about 500 meters. It is known to occur down at least to 1100 meters, and there is a somewhat questionable report of it from about 1495 meters (for details see Bigelow and Schroeder, 1948, p. 485). Depth records for other members of the genus have been from between 448 and 1024 meters.

Remarks. The few known species that fall in *Centroscyllium* as generally defined are set apart from all other known members of the subfamily Squalinae by their dentition, the teeth having 3-5 cusps in both jaws. In this respect they are approached the most nearly by *Etmopterus,* in which the uppers have 3-7 cusps, but the lowers have only one. In all other known members of the subfamily the teeth (uppers as well as lowers) have only one cusp.

The genus *Paracentroscyllium* was proposed by Alcock (1889, p. 379) for three juvenile sharks, 5¼ inches long, from the Bay of Bengal, allied to *Centroscyllium* except that they had "monocuspid teeth" and an "absolutely smooth integument." But the nakedness of the skin was clearly a juvenile character (this accords with conditions in **fabricii,* see p. 41); and the lateral cusps on the teeth seem merely to have escaped notice, for Alcock's (1896, p. 308) subsequent study of four additional specimens up to nearly one foot long from the Arabian Sea led him to emend his original diagnosis of *ornatum* to read "minute tricuspid teeth in both jaws" and body "covered with minute placoid deciduous scales." Accordingly, in 1896 (pp. 308, 310) he united *Paracentroscyllium* with *Centroscyllium.* Hence it was as a *Centroscyllium* that he pictured *ornatum* in 1900 (Pl. 35, figs. 1-1B, including a figure of one of its denticles). And Fowler's (1941, p. 252) revival of *Paracentroscyllium,* as a subgenus of *Centroscyllium,* for species in which the "caudal ends in point posteriorly, lower edge of fin without distinct posterior notch," (harking back, no doubt, to Regan's [1908, p. 40] key to the species of *Centroscyllium*), runs counter to Burkhardt's (1900, p. 567, fig. 8) illustration of one of Alcock's original specimens, for this shows the caudal as blunt-tipped and with a distinct (though shallow) subterminal notch.

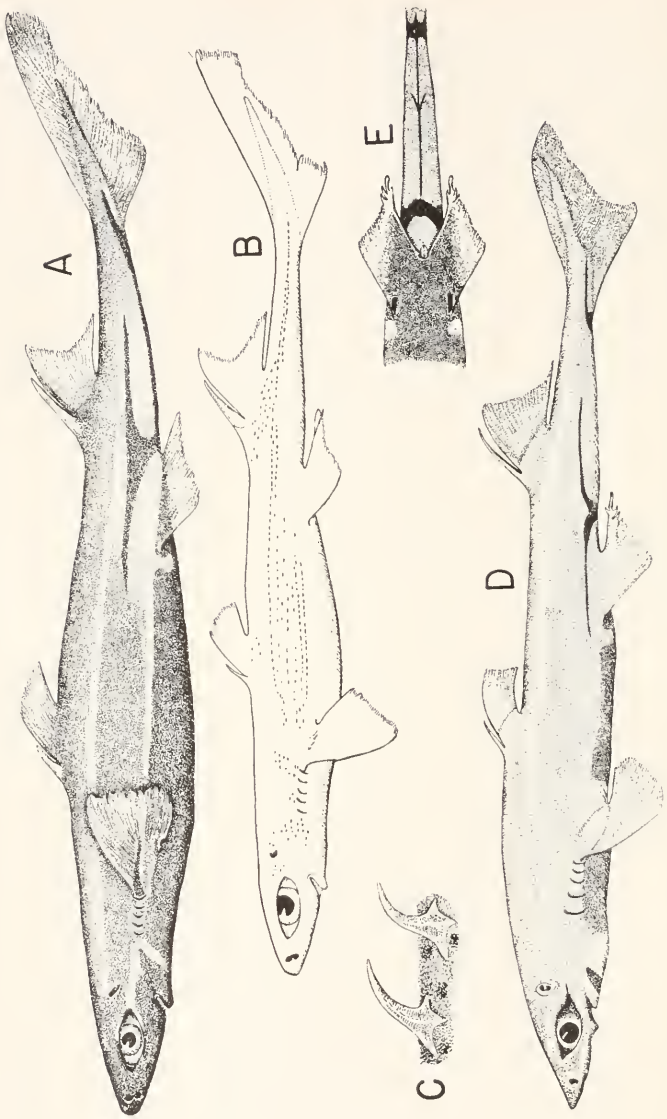

FIGURE 6

Species. The following supposedly separate species fall in *Centroscyllium*: **fabricii* Reinhardt 1825 (type species), both sides of the northern Atlantic; *granulatum* Günther 1887, Falkland Islands; *ornatum* Alcock 1889, Bay of Bengal and Arabian Gulf; **nigrum* Garman 1899 (incl. **ruscosum* Gilbert 1905), eastern Pacific off Panama (vicinity of the Galapagos, vicinity of Cocos Island), also Hawaiian region; and **ritteri* Jordan and Fowler 1903, Japan.

**C. fabricii,* the common "black dogfish" of English-speaking North Atlantic fishermen, has been described by several authors. Even so, examination of large catches made recently off the Nova Scotian coast (Bigelow and Schroeder 1954, p. 40) enables us to expand our earlier account (Bigelow and Schroeder 1948, p. 482) in the following respects. The teeth are already tricuspid in both jaws on specimens not more than 165 mm. long (suggesting that this is already the case at the time of birth), and the skin, then, is wholly naked above as well as below, just as Alcock (1889, p. 379) described it for the original (133 mm.) specimens of his *ornatum* from the Bay of Bengal. But a **fabricii* of 171 mm. already shows a dense band of denticles along the back, with a few on the upper part of the sides below the second dorsal fin. On one of 177 mm., the back as a whole, and the sides above the mid-level are rough with denticles, though the lower surface still is smooth. And the situation is much the same on one of 273 mm. But on specimens of 300 mm. and larger, the belly, like the upper parts, is strewn with denticles.

The color pattern, too, undergoes an interesting alteration with growth. The smallest specimen we have seen (165 mm. long) is ink-black below and slightly paler along the back and on the basal parts of the fins, with the two dorsals and the pectorals margined and the pelvics tipped with white, and with

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Fig. 6. A, *Etmopterus lucifer,* female 337 mm. long, Japan, Mus. Comp. Zool. No. 1109. B, outlines of juvenile male, 267 mm. long, Japan, Mus. Comp. Zool. No. 1123, to show the distribution of the black, presumably luminescent, markings. C, denticles from side of body below first dorsal fin of specimen shown in A, x about 35. D, *Etmopterus brachyurus,* male, 300 mm. long, Japan, after Smith and Radcliffe with the black markings added from the type specimen in the U. S. National Museum. E, ventral view of posterior part of trunk of same specimen.

white fin spines. The development of the denticles (see above) is accompanied by a paling to deep chocolate brown, first along the mid-zone of the back, then along the upper part of the sides, as illustrated by specimens of 171-177mm. (see above). The belly, however, continues black and the fins continue white-edged up to a length of 200-225 mm. But it is only the extreme tips of the dorsal fins that show any trace of white by the time a length of 280-330 mm. is reached, and all the fins on larger specimens are uniformly blackish right out to the margins. Meantime, the back and the upper part of the sides darken again after the dermal denticles have spread to the lower surface, so that half-grown specimens, and larger, are black above as well as below when taken from the water, unless the skin has been rubbed off, as often happens in the trawl. We have seen no exception to this rule among the many specimens we have handled during the cruises of "Caryn" and of "Capn. Bill II" during 1949, 1952 and 1953 (Bigelow and Schroeder 1954, p. 41). Our earlier account of the color of adult **fabricii* as "deep chocolate brown, darkest (almost black) below and on the fins generally" (Bigelow and Schroeder 1948, p. 485) was based on a specimen that had reposed for several years in alcohol.

We think it evident, from the foregoing, that changes with growth must be taken into account in any discussion of the possible taxonomic significance of fin-markings and of the regional distribution of dermal denticles in this particular genus.

The North Atlantic, Japanese, and Falkland Island representatives of the genus all seem to deserve continued recognition as separate species, though they resemble one another closely in general appearance. Thus the distance from the upper origin of the caudal fin to the rear end of the base of the second dorsal fin is as long as from the eye to the level of the 4th-5th gill openings in **ritteri* of which we have an excellent specimen at hand, about 425 mm. long (Fig. 7A), whereas in **fabricii* of about that same size the caudal peduncle (measured as above) is only about as long as from the eye to the first gill openings. This contrast, indeed, was invoked as alternative between the Japanese and North Atlantic populations in our earlier key to the species of *Centroscyllium* (Bigelow and Schroeder 1948, p. 482). The denticles, too, on specimens of about equal sizes are somewhat sparser on **ritteri* than on **fabricii;* as an illustration,

7 or 8 denticles on the side, below the first dorsal fin, counted along a nearly straight line, occupy a length of 1 cm. on our **ritteri* of 425 mm., but 8 to 12 denticles occupy this space on the specimens of **fabricii* of about 400 mm.

The general coloration of the body seems also to be distinctive here, for all the **fabricii* we have handled, large enough for the denticles to have spread to the lower surface (p. 41), have been plain above as well as below, not only when fresh but after a few years' stay in alcohol. But the two original specimens of **ritteri,* taken three years previous, are described as "uniform dark grayish brown, blackish below in front" (Jordan and Fowler, 1903, p. 635). And this applies equally to the alcoholic specimen of **ritteri* we have at hand, the lower surface of which is densely denticulate, while it also shows a definite black flank mark on either side of the rearward part of the trunk (Fig. 7A).

Judging from Burkhardt's (1900, p. 567, fig. 7) outline drawing of the type specimen (270 mm. long), *C. granulatum* Günther 1887, from the Falkland Islands, agrees more closely with **ritteri* than with **fabricii* in the length of the caudal peduncle relative to the dimensions of the head. But Günther's (1887, p. 7) characterization of the dermal denticles of *granulatum* as "much coarser" than those of **fabricii* "and in the form of granulations" sets it apart equally from **ritteri,* the thorn-like denticles of which (Fig. 7C) more nearly recall those of **fabricii* (Bigelow and Schroeder 1948, fig. 91), except that they are relatively somewhat longer and more slender.

With **ritteri* clearly separable from **fabricii,* and *granulatum* seemingly so, the same might have been expected to hold good for **nigrum* (including **ruscosum* Gilbert 1905) ; or at the least, a closer relationship might have been expected with **ritteri* than with **fabricii* on geographic grounds. Actually, however, **nigrum* is pictured both by Garman (1899, Pl. 1, fig. 2) and by Beebe and Tee Van (1941, p. 120, fig. 32), as falling with **fabricii* in the shortness of its caudal peduncle relative to the dimensions of the head, which we can corroborate from our examination of one of Gilbert's original Hawaiian specimens of his **ruscosum,* about 400 mm. long (the co-type), loaned us by the Stanford University Museum through the kind offices of Dr.

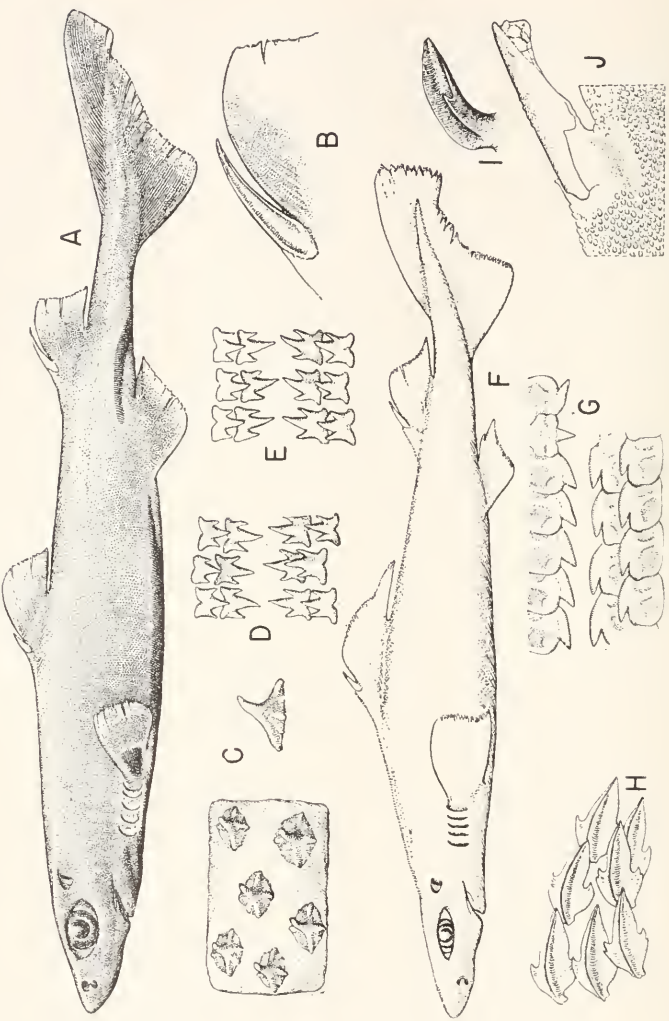

FIGURE 7.

George Myers,[9] and of the type specimen in the U. S. National Museum. Nor can we find anything in the dermal denticles to separate **nigrum* from **fabricii.*

Also, Garman's (1913, p. 230) use of the number of cusps on the lower teeth as alternative between **nigrum* (with five) and **fabricii* (with three) has failed to withstand the test of time, for most of the lowers midway along either side of the jaw actually have five cusps in **fabricii* (Bigelow and Schroeder 1948, p. 483, fig. 91E). And Beebe and Tee Van (1941, p. 121) have found that on their Cocos Island specimens of **nigrum* the outermost pair of cusps were not as prominent as pictured by Garman (1899, Pl. 4, fig. 6).

**C. nigrum,* however, maturing at a length of only about 400 mm. (Gilbert 1905, p. 581) or perhaps smaller still (Beebe and Tee Van 1941, p. 120) is a much smaller shark than **fabricii,* the males of which seemingly do not mature until at least 600 mm. long. Also, the pectoral and dorsal fins continue white tipped to maturity in **nigrum* (Gilbert 1905, p. 581, fig. 230; Beebe and Tee Van 1941, p. 120, fig. 32) though with the white areas somewhat reduced, whereas half-grown specimens of **fabricii,* and larger, show no trace of the white fin-markings that are so conspicuous on small specimens (p. 42). It may also prove (when more specimens have been examined) that it is characteristic for the pectorals to extend somewhat farther rearward in **nigrum* than in **fabricii,* for they are pictured both by

[9] The larger of Garman's original two specimens of **nigrum,* used as the basis for his account of the anatomy of the genus *Centroscyllium,* is now in a very fragmentary condition.

Fig. 7. A, *Centroscyllium ritteri,* female about 425 mm. long, Mus. Comp. Zool. No. 1370. B, second dorsal fin spine of same drawn to larger scale to show the longitudinal grooving. C, dermal denticles from side below first dorsal fin, x about 6 to 8. D, upper and lower teeth from central part of jaw, x about 4. E, upper and lower teeth from midway along side of jaw, x about 4. F, *Centrophorus foliaceus,* immature male, 351 mm. long, in U. S. Nat. Mus., from Japan. G, upper and lower teeth of same at center of mouth, x about 4. H, denticles of same from side below first dorsal fin, x about 13. I, lateral view of denticle, x about 18. J, *Centrophorus armatus,* southern Africa, second dorsal spine of specimen 330 mm. long, x about 3.5, from a photograph kindly contributed by Dr. J. L. B. Smith (see p. 6).

Garman (1899, Pl. 1, fig. 2) and by Beebe and Tee Van (1941, p. 120, fig. 32) as reaching nearly or quite to a perpendicular at the point of emergence (from the skin) of the first dorsal spine, which is true also of the Hawaiian specimen we have seen (mentioned above). It therefore seems justifiable to accept **nigrum* as a distinct species, at least until a larger number of specimens from the Pacific populations have been studied with a critical eye.

C. ornatum of the northern Indian Ocean falls with the *fabricii-nigrum-ritteri* group in its thorn-like denticles (Alcock 1900, Pl. 35, fig. 1). It agrees more nearly in proportional dimensions with **nigrum* of low latitudes in the eastern Pacific than with **ritteri* of the northwestern Pacific, the distance from the rear end of the base of its second dorsal fin to the origin of the upper side of its caudal fin being only about as long as from the eye to the first pair of gill openings, while its pectorals reach rearward about to a perpendicular at the point of emergence of the first dorsal fin spine. But Alcock (1896, p. 308) describes the fins as well as the trunk as "uniform jet black" on specimens nearly one foot long. Neither does his account of the type specimen, 133 mm. long, nor his illustration of it (Alcock 1894, Pl. 8, fig. 2) suggest any white fin-markings, such as are conspicuous on *nigrum* to maturity. While Regan (1908, pp. 40-41) characterized *ornatum* as without a distinct posterior notch on the caudal fin, seemingly following Alcock's (1894, Pl. 8, fig. 2) original illustration, Burkhardt's (1900, p. 567, fig. 6) drawing of one of the original series in the British Museum clearly indicates a subterminal notch. And Alcock's (1900, Pl. 35, fig. 1) second representation of the caudal of a larger specimen seems more fanciful than realistic, so widely does it differ from his earlier illustrations. With our knowledge of *ornatum* so far from adequate, and with the specimens of it in the collection of the Zoological Survey of India in a bad state of preservation (the late Dr. S. L. Hora has so written us in a recent letter), a final decision as to its status obviously is a matter for some future student. Meanwhile we believe a tentative key to the species of *Centroscyllium,* using the length of the caudal peduncle as the first alternative, seems likely to be more helpful for identification than our earlier key, in which the primary alternative is the location of the rear margin of the pectoral fin (when laid back) relative to the location of the first dorsal fin spine.

Provisional Key to Species of *Centroscyllium*

1. Distance from rear end of base of second dorsal fin to origin of upper side of caudal fin nearly or quite as long as from eye to level of origin of pectoral fins .....**ritteri* Jordan and Fowler 1903
   Japan (Fig. 7 A,B,C). p. 42

   Distance from rear end of base of second dorsal fin to origin of upper side of caudal fin only about as long as from eye to first-second gill openings 2
2. Dermal denticles on anterior part of trunk "in the form of granulations" (Günther 1887, p. 7) ..... *granulatum* Günther 1887
   Falkland Islands. p. 43

   Dermal denticles in the form of spines or thorns on stellate bases 3
3. Margin of pectorals, when laid back, falls short of a perpendicular at point of emergence from skin of first dorsal spine by a distance at least 25 per cent as long as eye .....**fabricii* Reinhardt 1825.
   North Atlantic. p. 41

   Margin of pectorals, when laid back, reaches nearly or quite to below point of emergence from skin of first dorsal spine 4
4. Dorsal, pectoral and pelvic fins white edged at all stages in growth **nigrum* Garman 1899
   (incl. *ruscosum* Gilbert 1905), eastern tropical Pacific off Central America, also Hawaiian region. p. 43.

   Fins, as well as body, black at all stages in growth ..... *ornatum* Alcock 1889
   Bay of Bengal and Arabian Gulf. p. 46

Genus ETMOPTERUS Rafinesque 1810

Etmopterus Rafinesque 1810, p. 14; type species *E. aculeatus* Rafinesque, Mediterranean, equals **Squalus spinax* Linnaeus 1758. Generic synonyms, see Bigelow and Schroeder 1948, p. 487.

Generic characters. Essentially as in *Centroscyllium* (p. 38), except with lower teeth much as in *Squalus*, i.e., much broader than the uppers and with only one cusp, the base of each tooth overlapping that of the next outward so that each row forms a continuous dental band, and with the cusps directed so strongly outward all along the jaw that their successive inner margins act as a nearly unbroken cutting edge (Bigelow, Schroeder and Springer 1953, figs. 7-10); dermal denticles on sides of body

ranging from thorn-like to bristle-like and to truncate, on quadrate bases.

Size. At maturity the various species of *Etmopterus* range in length from slightly more than 200 mm. (**virens,* perhaps also **villosus*) to a recorded maximum of 728 mm. in the case of **princeps* (Collett 1904, p. 4).

Depth range. The members of this genus are creatures of at least moderately deep water, where (as a group) their depth range is a wide one. The shoalest captures we find recorded for any of them are 73-91 meters for **spinax* in the northernmost parts of its range (Smitt 1895, p. 1165) and 183 meters for **abernathyi*, off New Zealand (Garrick 1957, p. 181); the deepest are 2074 meters for *E. princeps* (see Bigelow, Schroeder and Springer 1953, p. 251; Bigelow and Schroeder 1954, p. 47; and Grey 1956, p. 95 for details as to **princeps*). Most of the records for one species or another in various parts of the world have been from about 300 meters to about 900-1000 meters.

Remarks. These small, black-bellied deep-water sharks, of which some 16 recognizably distinct species are known, form a very compact unit. Characters that have proved the most useful for diagnosis of species within the genus are: the sizes and relative positions of the fins; the color pattern, whether uniformly as dark above as below or paler above with conspicuous dark flank markings of characteristic shape, whether or not with complex patterns of longitudinal bands of black dashes and dots (presumably luminescent) and whether with or not with white fin markings; also, for half-grown specimens and larger, the shapes of the dermal denticles, and their arrangement. But in using the denticles for diagnosis allowance must be made for the size of the specimens in question, for we have found that in one species (**princeps*) where the denticles are bristle-like on very young specimens, they are succeeded by thorn-like forms on half-grown individuals and larger (Fig. 3, F, G).

For accounts of the luminescent organs (for the species that have them) and of luminosity in this genus, see Johann (1899) and Oshima (1911).

Whitley (1939, p. 266) has revived the genus *Acanthidium* Lowe 1839, type species **A. pusillum* Lowe 1839 (=*Centrina nigra* Lowe 1834, preoccupied), designated by Jordan and Evermann (1896, p. 55), as distinct from *Etmopterus* Rafinesque

1810, type species *E. aculeatus* Rafinesque, (=**Squalus spinax* Linnaeus 1758). And Fowler (1941, p. 251) has recognized two corresponding subgenera within the genus *Etmopterus,* namely *Acanthidium* Lowe 1839, with "second dorsal origin behind ventral base; first dorsal origin midway between orbit and second dorsal origin," and *Etmopterus* Rafinesque 1810 with "second dorsal origin over or a little before ventral base; ventral origin slightly nearer subcaudal origin than pectoral origin." But these differences do not seem to us wide enough for generic — or even subgeneric — separation (p. 22; Bigelow, Schroeder and Springer 1953, p. 238). *Acanthidium* as employed by Garman (1913, p. 215) in a different sense, is discussed on p. 21.

Species. The genus *Etmopterus* is especially interesting from the taxonomic standpoint, because it is already known to include a larger number of recognizable species than we have any reason to suppose is included in any other genus of squaloid sharks. These species, it is true, resemble one another so closely in general aspect that any one of them might easily be mistaken for any other, on cursory inspection. But closer examination has shown that they are sharply separated by differences both in the relative positions of the fins and in the nature and arrangement of the dermal denticles, and also in the color pattern which has proved a much more convenient species-character here than it is usually thought to be among other sharks.

The following seven species have been known from the North and Equatorial Atlantic, including the Mediterranean and the Gulf of Mexico.

1. **spinax* Linnaeus 1758, type species of the genus (many of the reports of it have been as *niger* Cloquet 1820, p. 93); eastern North Atlantic (including the Mediterranean) from the Cape Verde Islands, Morocco and the Azores to Norway.

2. **pusillus* Lowe 1839 (=*Centrina nigra* Lowe 1834, but *nigra* is preoccupied in *Etmopterus* by *niger* Cloquet 1820, proposed in substitution for *spinax* Linnaeus 1758 and employed by many subsequent authors); tropical-subtropical Atlantic, from tropical West Africa to the Canaries, Madeira, and the Azores in the east (including the Mediterranean) and Gulf of Mexico in the west, where it has been found recently (Bigelow, Schroeder and Springer 1955, p. 2). The Japanese shark described and pictured under the name *pusillus* by Tanaka (1912,

Pl. 22; 1912[a], p. 88) was based on a clearly separable form (see below, p. 58).

3. **hillianus* Poey 1861, Cuban-West Indian region, northward to the offing of Chesapeake Bay.

4. **princeps* Collett 1904, both sides of the North Atlantic, Faroes-Hebrides region and offing of Gibraltar in the east; continental slope in the west where it is common from the offing of southern Nova Scotia to that of southern New England (Bigelow and Schroeder 1954, p. 46).

5. **polli* Bigelow, Schroeder and Springer 1953, equatorial West Africa.

6. **schultzi* Bigelow, Schroeder and Springer 1953, northern part of the Gulf of Mexico.

7. **virens* Bigelow, Schroeder and Springer 1953, northern part of the Gulf of Mexico.

For the diagnostic characters of the members of this group, see Bigelow, Schroeder and Springer 1953, p. 237.

An eighth North Atlantic *Etmopterus*, from the east coast of Florida, is described here as a new species, **E. bullisi*.

Etmopterus bullisi n. sp.

Figure 5 A-D

Plate 2

Type specimen. Female, 196 mm. long; "Pelican" Sta. 42, off northeast coast of Florida, Lat. 30°02′ N, Long. 80°05′ W; 205 fathoms (U. S. Nat. Mus. No. 158186).

Additional material: female of 205 mm. and immature male of 230 mm. from this same locality; also immature male of 212 mm., "Pelican" Sta. 51, off eastern Florida, Lat. 29°48′ N, Long. 80°09′ W, about 200 fathoms.

Description. Proportional dimensions in per cent of total length of type specimen, and of a male 230 mm. long, to nearest 0.1 per cent.

Snout length in front of: outer nostrils 2.5, 2.8; mouth 11.7, 12.2.
Eye: horizontal diameter 4.6, 4.6.
Mouth: breadth 7.1, 7.0.
Nostrils: distance between inner ends 2.8, 2.8.
Gill openings: lengths first 2.3, 1.7; third 2.3, 1.7; fifth 2.0, 1.5.

First dorsal fin: vertical height 3.1, 2.8; length of base 4.6, 4.4.
Second dorsal fin: vertical height 4.6, 4.4; length of base 7.4, 7.0
Caudal fin: upper margin 24.0, 23.5.
Pectoral fin: outer margin 11.0, 10.0; inner margin 4.8, 5.6, width 4.6, 5.2.
Distance from snout to: 1st dorsal 33.7, 33.0; 2nd dorsal 56.6, 57.9; upper caudal 76.0, 76.5; pectorals 25.0, 24.4; pelvics 51.5, 50.0.
Interspace between: First and second dorsals 18.3, 18.7; 2nd dorsal and caudal 12.7, 13.9; base of pelvics and caudal 18.9, 20.4.

20 18
Teeth: —, —
27, 31

Description of type specimen. Trunk noticeably slender, its height at pectorals (where highest) about 12 per cent as great as its length to upper origin of caudal fin, its greatest thickness about equal to its greatest height; body narrowing rearward with caudal peduncle nearly as thick as high. Head flattened above, its length to origin of pectorals occupying about 33 per cent of trunk to origin of caudal fin.

Snout obtusely wedge-shaped anteriorly, its length in front of mouth about 50 per cent as great as length of head to origin of pectorals, its length in front of eyes about 28 per cent. Eye about 1.4 times as long as high, its horizontal diameter about 40 per cent as long as snout to mouth. Nostril with outer end close to edge of snout; anterior narial flap triangular, with pointed tip, reaching across narial opening. Pores on lower surface of snout so small that they are visible only on close scrutiny. Mouth low-arched, occupying about 80 per cent of breadth of head. Preoral clefts short, extending about 33 per cent the distance from corners of mouth toward nostrils. Furrows from corners of mouth reaching rearward half way toward first gill openings.

First gill openings a little shorter than distance between nostrils; fifth openings a little shorter than first to fourth; anterior margins only slightly concave, but tips of filaments exposed in first to third. Teeth smooth edged as in other members of this genus; uppers with only 3 cusps, the axial much the largest. Lowers with cutting edge nearly parallel with general trend of the jaw. Cusp of the median lower tooth, identified as such by its base overlapping that of the next tooth on either side, directed strongly outward, to the one side or the other, on all specimens seen. Two or three rows functional in upper jaw but one row only in lower jaw.

Dermal denticles low, conical-thorn-like, erect or nearly so and so sharp that the skin feels very rough. Denticles on lower surface straight, or nearly so, in random arrangement, but those on sides and back slightly curved rearward and arranged in single series in regular longitudinal rows (Pl. 2); the rows on the back anterior to the first dorsal fin converging rearward, but the rows on the sides paralleling in general the main axis of the trunk as far rearward as abreast the second dorsal, whence those above the mid-level trend downward-rearward along the tail sector and out along the caudal axis. The lower surface of the trunk, like sides and back, is closely set with denticles, except for the chin, the lips, a small area in the midline of the snout close in front of the mouth, and the margins of the nostrils, which are naked. Fins as a whole naked.

Base of first dorsal fin about as long as eye, its origin posterior to the origin of the pectorals by a distance about as long as from tip of snout to mouth. Rear end of base of first dorsal about equidistant between perpendiculars at axil of pectorals and at origin of pelvics. Distance from point of emergence from skin of first dorsal spine to point of emergence of second dorsal spine about as long as head to origin of pectorals. Second dorsal spine about 1.8 times as long as first, each measured from point of emergence from the skin, its tip reaching about 75 per cent toward the upper corner of the fin. Distance from rear end of base of second dorsal fin to origin of upper side of caudal fin about 54 per cent as long as between points of emergence from skin of first and second spines, and about 47 per cent as long as length of head to pectorals; upper side of caudal fin about as long as head to origin of pectorals, its shape as pictured in Figure 5A. Lower anterior margin of caudal 43 per cent as long as upper margin. Distance from origin of lower side of caudal fin to rear end of bases of pelvics about 75 per cent as long as head to origin of pectorals. Rear end of bases of pelvics a little anterior to point of emergence, from skin, of second dorsal spine. Pectorals truncate, with rounded corners, the distal margin, when laid back, falling about abreast of point of emergence from skin of first dorsal spine.

In their present state the edges of the pectorals, dorsals, and pelvics, and the terminal sector of the caudal, are much frayed out on all the specimens. But close examination makes it evident

that, normally, they are entire, not fringed as they are on **E. schultzi* (Bigelow, Schroeder, and Springer, 1953, p. 254, Fig. 9D).

Claspers of mature males not yet seen.

Color. Upper parts in general very dark sooty gray, the midline of the back paler (as a definite band on one of the specimens), with a vaguely outlined pale yellowish spot on the top of the head between the eyes. Lower surface of head and body sectors black; the black extending rearward in a narrow band along the lower surface of the tail sector, nearly or quite as far as the origin of the caudal; also upward on each side close behind the pelvics, to continue forward as a flank mark of the shape shown on Figure 5A. The pattern of coloration, however, is evident only on close examination, the sides, as a whole, being very nearly as dark as the belly. Distal parts of the dorsal, pectoral and pelvic fins, and lower edge of caudal pale gray after preservation, perhaps whitish in life.

The (presumably) luminescent system of markings to be seen on various other members of *Etmopterus* is evident here only as a row of black dots along the midline of the back from nape to base of caudal. If similar markings are present elsewhere they are masked by the dark hue and dense pigmentation of the sides.

Size. The size at maturity is not yet known.

Geographic range. So far known only off the northeast coast of Florida, at the localities listed above (p. 50).

Remarks. The linear arrangement of the denticles on its back and sides marks **bullisi* off from all the other species of *Etmopterus* that were known previously from the North Atlantic and Gulf of Mexico. It differs further from **spinax* in its stouter, thorn-like denticles, and in that the interspace between its first and second dorsal fins is only about as long as from tip of snout to first gill openings (as long as from tip of snout to origin of pectorals in **spinax*); from **hillianus* and from **virens* in its noticeably shorter caudal peduncle, relative to the length of the head; from **pusillus* in its thorn-shaped denticles (truncate with concave crown in **pusillus*); from **schultzi* both in the nature of the margins of its fins (p. 52) and in a relatively shorter caudal fin (upper margin only as long as from tip of snout to origin of pectorals in **bullisi*, but as long as from snout to rear edge of pectorals in **schultzi*); from **princeps* in a noticeably

longer interspace between its second dorsal and the origin of the upper side of its caudal (to mention only the most conspicuous difference); and from **polli* in its tricuspid upper teeth (mostly with 5 cusps in **polli*), in the roughness of the lower side of its snout, and in the minuteness of the pores there.

Among species known from other seas, it agrees with **lucifer* (originally described from Japan) in the linear arrangement of the denticles on the sides of the head and body, and in their thorn-like nature, also with **villosus* of Hawaiian waters; with **brachyurus*, originally described from the Philippines (p. 59); and with **abernathyi*, from New Zealand. But there is no danger of confusing it with either one of these for the following reasons: the distance from the tip of its snout to its first dorsal fin spine is shorter relatively than in **villosus* but its caudal fin is considerably longer; the upper margin of its caudal is much longer relatively than in **brachyurus;* the interspace between its two dorsal fins (not longer than from tip of snout to first gill openings) is noticeably shorter than in either **lucifer* or **abernathyi* (at least as long as from tip of snout to origin of pectorals), and its flank marks are much less conspicuous (cf. Fig. 5A with Fig. 6A) than in either of these last two.

The Mediterranean shark, also, that was named *Squalus infernus* by Blainville (1825, p. 59), a century and a quarter ago, is referable to *Etmopterus* by Blainville's account of its upper teeth as three-cusped, but of its lowers as one-cusped, with horizontal cutting edge.[10] And there is nothing in the dimensions given for it by Blainville to set it apart from **E. spinax,* as appears from the accompanying comparative table. Our earlier statement (Bigelow, Schroeder and Springer 1953, p. 224) that its proportional dimensions differ from those of other Atlantic species was based on a misreading of the measurements given for it by Blainville.

> Proportional dimensions in per cent of total length (A) for the type specimen, 255 mm. ("dix pouces") long, of *infernus* Blainville 1825; and (B) for a female **spinax,* about 285 mm. long, from the Mediterranean, in the Museum of Comparative Zoology.

[10] Notwithstanding its tooth characters, Garman (1913, p. 197) classed it as a synonym of **Centrophorus uyato* Rafinesque 1810. We may also point out that Blainville's (1825, p. 59) reference for it to his "Pl. 14, Fig. 2" was incorrect; actually this figure represents a **Lamna nasus.*

	A	B
Snout to 5th gill openings	19	21
Snout to cloaca	57	58
Snout to 1st dorsal fin	31	32
Snout to 2nd dorsal fin	63	63
Cloaca to lower origin of caudal fin	23	19

**S. spinax* has been reported from southern Africa as well as from the North Atlantic and Mediterranean, on the evidence of a shark that was taken off Cape Point by the "Pickle" (Gilchrist 1922, pp. 42, 49; Barnard 1925, p. 51; Smith 1949, p. 59), with two others taken in the same general region by the "Discovery" (Norman 1935, p. 37). And the "Pickle" specimen certainly falls with **spinax* in the relative positions of its fins, as well as in the bristle-like nature and irregular distribution of its dermal denticles, to judge from what little information is available. But we still await a detailed description of it (or of the specimens taken by "Discovery"); nor are the outlines of the black belly area and of the flank-markings shown on Smith's illustration. Final decision, in short, as to the specific relationship that the *spinax*-like form of South African waters bears to the typical **spinax* of the northeastern Atlantic must await a comparison of specimens from the two ocean areas. None of the other Atlantic species has been reported from farther southward in the southern hemisphere that latitude 6°08′S (*S. polli* Bigelow, Schroeder and Springer 1953, p. 241).

Other named sharks that can be definitely placed in *Etmopterus* are the following.

E. granulosus (Günther) 1880, originally reported from the southwest coast of South America, and subsequently from Argentina (Lahille 1921, p. 16, by name only) as well as from southern Africa (Gilchrist 1922, p. 41; Barnard 1925, p. 49; Smith 1949, p. 58). Barnard's reference of it to the Hawaiian Islands, without supporting date, may actually have referred to **E. villosus*. The chief diagnostic features of *granulosus* are: distance from tip of snout to emergence from skin of first dorsal spine is at least as long as from emergence of first dorsal spine to rear end of base of second dorsal (Günther 1880, Pl. 2, fig. C; Barnard 1927, Pl. 2, fig. 8; Smith 1949, p. 58, fig. 50); distance from rear end of base of pelvics to origin of lower side of caudal is shorter than from tip of snout to first gill openings;

margin of pectorals (when laid back) reaches nearly to abreast of base of first dorsal spine; dermal denticles on sides of body described as granular, without median spine and in irregular pattern, but those on tail in the form of minute spines and arranged in longitudinal bands (Günther 1880, p. 19); body uniformly dark brown to blackish, but the fins edged with white (Günther 1880, p. 19), a feature not mentioned either by Barnard or by Smith. Incidentally, the upper side of the caudal fin is shown as about as long as from the tip of the snout to the origin of the pectoral fins both by Günther (1880, Pl. 2, fig. C) and by Barnard (1927, Pl. 2, fig. 8), but only as long as from snout to first gill openings by Smith (1949, p. 58, fig. 50), a disagreement we cannot resolve.

**E. lucifer* Jordan and Snyder 1902, Japan (Fig. 6 A-C). The chief diagnostic features, as appear both from the original account and from our own examination of 5 specimens (two in the Museum of Comparative Zoology, three in the U. S. National Museum) are: distance from tip of snout to point of emergence from skin of first dorsal spine is about as long as from emergence of first dorsal spine to midpoint of base of second dorsal; upper side of caudal and distance from rear end of base of pelvics to origin of lower side of caudal both are about as long as from tip of snout to origin of pectorals; rear end of base of first dorsal is about midway between perpendiculars at origin of pelvics and at axil of pectorals; dermal denticles slender, thorn-like, weakly curved, sloping only slightly, and close set; those on the sides arranged in general in longitudinal rows and directed downward-rearward (a conspicuous feature), but those on the black areas of the lower surface in random pattern, directed obliquely downward-rearward on either side of the body toward the midline, where a single row is directed rearward. Upper surface of head, anterior to spiracles, with extensive naked areas. Back and upper part of sides chocolate brown; lower surface black, with a distinctive black marking on either flank (Fig. 6A; Bigelow, Schroeder and Springer 1953, fig. 6B), the line of transition from black to brown marked by a pale band as shown on Figure 6A. Imposed on the sides, there is also a complex pattern of black dash-like markings, presumably luminescent (Fig. 6B; Oshima 1911, pp. 1-3), in longitudinal linear arrangement.

Originally described from Japan, **lucifer* has since been found in South African waters (Gilchrist 1922, p. 49; Barnard 1925, p. 50; Norman 1935, p. 37; Smith 1949, p. 59, fig. 52). It has also been reported by name from the Philippines (Smith and Radcliffe 1912, p. 679, 21 specimens; Fowler 1941, p. 248). and from Flores Straits in the East Indies (Weber 1913, p. 597). But we think it more likely on geographic grounds that these reports from equatorial waters actually were based on **E. brachyurus* (p. 58).

**E. villosus* Gilbert 1905, from the Hawaiian Islands. The combination of slender, spine-like denticles (those on back and sides in linear series) with a first dorsal fin standing so far rearward that its point of origin is about midway between the tip of the snout and the origin of the upper side of the caudal fin (corroborated by our examination of the type specimen in the U. S. National Museum), sets **villosus* apart from all other members of the genus yet known. Other features diagnostic of **villosus* are: upper side of caudal about as long as from tip of snout to first-second gill openings; distance from rear end of pelvics to origin of lower side of caudal fin only a very little longer than from snout to level of spiracles; rear end of base of first dorsal about midway between origin of pelvics and rear margin of pectorals when the latter are laid back; abdomen and lower side of head blue-black, the sides brown, no black flank marks being suggested by Gilbert's (1905, Pl. 66) illustration or by our recent examination of the type specimen; dorsals, pectorals and pelvic fins broadly edged rearward with white; lower surface in general rough with denticles, the skin being naked only on the lips and nostrils, close around the eyes and spiracles, and close behind the dorsal, pectoral and pelvic fins, which are partially so; the denticles along the back and on the tail arranged in lengthwise series. On the type specimen, the denticles along the midline of the lower surface are smaller than they are pictured; the first dorsal spine is only about 65 per cent as long as the second; the upper teeth have only three cusps; and the cusps of the lower teeth are so strongly oblique that their inner margins are nearly parallel with the jaw.

**Villosus* is so far known only from the type specimen, 170 mm. long, taken by the "Albatross" off the south coast of Molokai (Gilbert 1905, p. 580, Pl. 66).

E. frontimaculatus Pietschmann 1907, from Japan. In general, this species resembles **E. lucifer* in color, with brown back and sides contrasting with ink-black belly and black flank marks. But the latter differ in shape from those of **lucifer,* as Oshima (1911, p. 2, fig. 1) has pointed out, while neither Pietschmann's account nor his illustration (1908, p. 657, Pl. 1, fig. 2) suggest the presence of the linear pattern of luminous organs to be seen on the sides of the body in **lucifer* (p. 56). *E. frontimaculatus* is set apart still more sharply from **lucifer* by its denticles, which (as pictured by Pietschmann 1908, p. 657, figs. 1, 2) are truncate, with concave crowns (slender, thorn-like in **lucifer,* p. 56), while those on the sides are arranged irregularly (in linear series in **lucifer*). Also, according to Pietschmann (1908, pp. 656-657) the skin of *frontimaculatus* is naked on the black areas of the lower surface and of the tail, which in **lucifer* (p. 56) are as densely denticulate as the paler sides are and the back. *E. frontimaculatus* resembles **E. pusillus* of the Atlantic in the nature of its denticles; Tanaka, in fact (1912, Pl. 22, 1912[a], p. 88) pictured and described a specimen from Misaki under that name. But it differs sharply from **pusillus* in the nakedness of the black areas on its lower surface and on its tail; in a somewhat more rearward position of its first dorsal fin relative to the pectorals, and — more conspicuously — in its color pattern, for the black belly and flank marks contrast with paler brown sides and back which is not the case in **pusillus* (compare Pietschmann 1908, Pl. 1, fig. 2 with Bigelow, Schroeder and Springer 1955, p. 3, fig. 1). *E. frontimaculatus* is so far known only from Japan.

**E. brachyurus* Smith and Radcliffe 1912 from the Philippines. This shark (Fig. 6 D, E) falls with **lucifer* in the relative position of its pectoral, dorsal and pelvic fins; in the thorn-like nature of its dermal denticles (these roughen the lower surface of its body as well as the upper); and in the arrangement in longitudinal bands of those on the upper surface, on the caudal peduncle, and on the bases of the fins. It falls further with **lucifer* in its general color pattern, with sharply outlined black flank markings, which are not shown on Smith and Radcliffe's original illustration of it. But it differs from **lucifer* in a relatively much shorter caudal fin, the upper margin of which is only about 66 per cent as long as from the tip of the snout to

the origin of the pectorals, as we can verify from recent examination of the type specimen in the U. S. National Museum (about as long as from snout to pectorals in **lucifer*). And there are five cusps on its upper teeth (three in **lucifer*), with the laterals longer, relative to the median member, than in **lucifer*. **E. brachyurus* was originally described from an adult male, 227 mm. long, taken off Jolo Island in the Philippines by "Albatross" in 1909, from 481 meters (263 fathoms). But its range extends to southern Australia, provided our union with it of *molleri* Whitley 1939 be correct (see below).

E. molleri (Whitley) 1939, from Australia. This shark described by Whitley as *Acanthidium molleri,* seems not to differ from *E. brachyurus* in any significant respect, to judge from Whitley's description or illustration (Whitley 1939, p. 265, fig. 1; 1940, pp. 147-148, fig. 163).

E. baxteri Garrick 1957, from New Zealand. This newly described *Etmopterus*, known from a female 742 mm. long, caught at 914 meters (500 fathoms) seven miles south of Kaikoura, N. Z., finds a close counterpart in *E. princeps* of the North Atlantic. But it differs so sharply from *princeps* in the respects summarized in the accompanying key (p. 63, alternatives 14-15), that the two clearly represent distinct species.

E. abernathyi Garrick 1957, from New Zealand. This well defined species, described from an immature male 338 mm. long and from a female 278 mm. long, caught at 183-366 meters off Kaikoura, N. Z., falls in the subdivision of the genus that is characterized by slender thorn-like denticles, with those on the upper part of the sides arranged in unilinear, longitudinal rows, and by a conspicuous pattern of black markings. Among the other members of this division it comes the closest to *brachyurus*. But it is separated from the latter by a much longer caudal fin and by a more forward position of the first dorsal fin, to mention only the most conspicuous differences (see Key, pp. 61, 62, alternatives 7-10). For comparison with other members of its genus, we refer the reader to Garrick's detailed account of *abernathyi* and to his excellent illustrations of it.

The U. S. National Museum also contains a female *Etmopterus*, about 270 mm. long (U.S.N.M. No. 91576) collected among the Galapagos by the "Albatross" in 1888, from 717 meters (392 fathoms), which agrees very closely with the West African

**polli*, except that such of its upper teeth as are still intact have only three cusps, contrasting with five cusps in **polli*. Unfortunately the specimen is now in such poor condition that we dare do no more than call attention to the presence in Galapagan waters of a species of *Etmopterus*, as yet undescribed.

Finally, we face the case of *E. paessleri* Lönnberg (1907, p. 5, fig. 2) from the Straits of Magellan. Lönnberg's reference of this shark to *Etmopterus* has been accepted both by Regan (1908, p. 43) and by Garman (1913, p. 229). And while Lönnberg states that lateral cusps were not visible ("nicht sichtbar") on its upper teeth, the type (and only known) specimen was so small (about 160 mm. long) that these structures may have been overlooked. Until this point can be settled its generic status must remain open. Meantime, we are content to let this species rest provisionally in *Etmopterus*. Whatever the final outcome in this regard, *paessleri* is set apart from all other members of *Etmopterus* by the nature of its dermal denticles, which are described (they have not been pictured) as having a large central spine, surrounded by several smaller spines ("einen grosseren Stachel und mehere kleinere Nebenstacheln," Lönnberg 1907, p. 5). Also, its second dorsal fin-spine is described as a little smaller than the first, just the reverse of the usual relationship.

Key to species of *Etmopterus*

1. Dermal denticles with larger central spine surrounded by several smaller spines; second dorsal fin spine smaller than first dorsal spine; lateral cusps not easily visible on upper teeth of small specimens ..... *paessleri* Lönnberg 1907.
   Straits of Magellan. p. 60

   Dermal denticles either truncate or with a central spine only, the latter bristle-like or thorn-like; second dorsal fin spine longer than first dorsal spine; lateral cusps on upper teeth clearly visible, even on very small specimens 2
2. Upper margin of caudal fin nearly as long as from tip of snout to rear edge of pectorals when these are laid back ..... **schultzi* Bigelow, Schroeder and Springer 1953.
   Northern part of Gulf of Mexico. p. 50

   Upper margin of caudal fin very little (if any) longer than from tip of snout to origin of pectorals and considerably shorter in most 3
3. Dermal denticles on sides of body truncate, without central spine 4
   Dermal denticles on sides of body with a central spine, either conical,

thorn-like, or bristle-like. 6

4. Back and upper part of sides dark brown, contrasting sharply with a black marking on either flank, and with lower surface of head and body; the black areas partially naked. .....*frontimaculatus* Pietschmann 1907. Japan. p. 58

Back and upper part of sides black or sooty like lower surface; no conspicuous flank-markings; lower surface, like upper, rough with denticles. 5

5. Denticles on sides of tail not arranged in regular longitudinal rows, and of same shape as those on sides of body; interspace between first and second dorsal fins about as long as from tip of snout to axil of pectorals .....**pusillus* Lowe 1839. p. 49 Eastern Atlantic from equatorial West Africa to the coast of Portugal, including the Cape Verde Islands, the Canaries, Azores and Madeira; also Gulf of Mexico. p. 49.

Dermal denticles on tail arranged in longitudinal rows, and more spine-like than those on the body; interspace between first and second dorsal fins shorter than from snout to first gill openings ..... *granulosus* Günther 1880. Coast of Chile, also reported from Natal coast of southern Africa and from Argentina. p. 55.

6. Denticles on sides in definite uniserial longitudinal rows 7

Denticles on sides in random arrangement, not in longitudinal rows ..11

7. Upper side of caudal fin at least not longer than from tip of snout to second gill openings. 8

Upper side of caudal fin about as long as from tip of snout to origin of pectorals. 9

8. Distance from tip of snout to first dorsal spine is about as long as from base of first dorsal spine to origin of upper side of caudal; interspace between first and second dorsal fins is only about as long as from tip of snout to level of spiracles. .....**villosus* Gilbert 1905. Hawaiian Islands. p. 57.

Distance from tip of snout to first dorsal spine is little longer than from first dorsal spine to rear end of base of second dorsal fin; interspace between first and second dorsal fins is at least as long as from tip of snout to second gill openings. ..... **brachyurus* Smith and Radcliffe 1912. Philippines; apparently including *E. molleri* (Whitley) 1939, southern Australia. p. 58.

9. Interspace between first and second dorsal fins is much shorter than from snout to first gill openings; black flank markings not conspicuous ..... **bullisi*, new species, off northeast coast of Florida. p. 50

Interspace between first and second dorsal fins is as long as from tip of snout to origin of pectorals, or longer; black flank markings conspicuous. 10

10. Distance from base of pelvics to origin of lower side of caudal is only about as long as from tip of snout to first gill openings ..... **abernathyi* Garrick 1957. New Zealand, p. 5

Distance from base of pelvics to origin of lower side of caudal is as long as from tip of snout to origin of pectorals .....**lucifer* Jordan and Snyder 1902. Japan; Atlantic off southern Africa; also reported by name from Argentina, the Philippines and the East Indies. p. 56.

For list of Philippine, East Indian, and South African records, see Herre 1953, p. 30.

11. Distance from rear end of base of pelvics to origin of lower side of caudal is at least as long as from axils of pectorals to origin of pelvics. 12

Distance from rear end of base of pelvics to origin of lower side of caudal is only about ½ as long as from axil of pectorals to origin of pelvics. 14

12. Distance from origin of pectorals to origin of pelvics is not longer than from tip of snout to origin of pectorals. .....**polli* Bigelow, Schroeder and Springer 1953. tropical West Africa. p. 50

Distance from origin of pectorals to origin of pelvics is longer than from tip of snout to origin of pectorals. 13

13. Denticles on sides below first dorsal fin are slender, bristle-like (Bigelow, Schroeder 1948, Fig. 92B); skin on lower surface of snout and in region of gill openings is rough with denticles; snout in front of spiracles about as long as from spiracles to level of axil of pectorals; black flank markings as in Figure 5H. ..... **hillianus* (Poey) 1861. Cuban and West Indian region, and northward along the American slope to the offing of Chesapeake Bay. p. 50.

Denticles on sides below first dorsal fin low, conical (Bigelow, Schroeder and Springer 1953, Fig. 10, D, E); skin on lower surface of snout

and in region of gill openings naked; snout in front of spiracles only about as long as from spiracles to level of origin of pectorals; black flank markings as in figure 5G. .....*virens* Bigelow, Schroeder and Springer 1953. Northern part of Gulf of Mexico. p. 50

14. Interspace between first and second dorsal fins is longer than from tip of snout to axil of pectorals; distance from rear end of second dorsal to origin of upper side of caudal is only about 35 per cent as long as interspace between first and second dorsals. ..... *baxteri* Garrick 1957. New Zealand. p. 59

Interspace between first and second dorsal fins is only about as long as from tip of snout to origin of pectorals; distance from rear end of second dorsal to origin of upper side of caudal is about 50 per cent as long as interspace between first and second dorsals. 15

15. Dermal denticles on sides slender, bristle-like, and closely spaced (Fig. 3E); breadth of head about as great as length of snout to mouth; longest gill openings only 14-33 per cent as long as eye; black flank marks conspicuous, of shape shown in Figure 5F....*spinax* (Linnaeus) 1758. Eastern Atlantic, including Mediterranean, from the Cape Verde Islands, Morocco and the Azores to Norway, p. 49; also reported from southern Africa. p. 56.

Dermal denticles on sides low, conical to thorn-like (more slender on juveniles), and more loosely spaced (Fig. 3, F, G); breadth of head 1.2-1.4 times as great as length of snout (to mouth); longest gill openings 33-50 per cent as long as eye; flank markings not conspicuous, if visible at all. .....*princeps* Collett 1904. Faroes-Hebrides region and offing of Gibraltar in eastern Atlantic; offing of southern Nova Scotia to offing of southern New England in western. p. 50.

Genus CENTROPHORUS Müller and Henle 1837

Centrophorus Müller and Henle 1837, p. 398; 1937A, p. 115; 1841, p. 89; type species **C. granulosus* Müller and Henle, Mediterranean, considered by them and by subsequent authors in general as the same as *Squalus granulosus* Bloch and Schneider 1801, no locality given.

Generic Synonyms:

Squalus in part, Bonnaterre, 1788, p. 12, for **S. squamosus* Bonnaterre,

type locality not known; Bloch and Schneider 1801, p. 135 for **S. granulosus* Bloch and Schneider, no stated locality.

Acanthorhinus in part, Blainville 1816, p. 121, for **A. squamosus* Blainville, equals *Squalus squamosus* Bonnaterre 1788, and *A. granulosus* Blainville, equals **Squalus granulosus* Bloch and Schneider 1801.

Centrina in part, Cuvier 1817, p. 130, for *C. squamosus* Cuvier, equals **Squalus squamosus* Bonnaterre 1788.

Lepidorhinus Bonaparte 1838, type and only included species, **Squalus squamosus* Bonnaterre 1788.

Acanthias in part, Müller and Henle 1841, p. 85, for *A. uyatus* Müller and Henle, equals **Squalus uyato* Rafinesque 1810, Mediterranean.

Spinax in part, Bonaparte 1841, Pl. 57, for *Spinax uyatus* Bonaparte, equals **Squalus uyato* Rafinesque 1810.

Machephilus Johnson 1867, p. 713, type and only included species *M. dumerili* Johnson, Madeira.

Entoxychirus Gill 1862, p. 498, type and only included species *E. uyatus* Gill, equals **Squalus uyato* Rafinesque 1810.

Gaboa (subgenus of *Centrophorus*) Whitley 1940, p. 145, type and only included species, **Centrophorus harrisonii* McCulloch 1915, Victoria, Australia.

Somnispinax (subgenus of *Centrophorus*) Whitley 1940, p. 146, type and only included species, *Centrophorus nilsoni* Thompson 1930, New Zealand.

Probable Generic Synonym:

Atractophorus Gilchrist 1922, p. 48, type and only included species *A. armatus* Gilchrist, off Natal, southern Africa. For discussion, see p. 82.

Not *Squalus* Linnaeus 1758, type species *S. acanthias* Linnaeus.

Not *Spinax* Cuvier 1817, p. 129, type species *Squalus acanthias* Linnaeus 1758.

Not *Acanthias* Risso 1826, p. 131, type species *A. vulgaris* Risso, Mediterranean, equals *Squalus acanthias* Linnaeus 1758.

Generic characters. Squalinae with the fin spines laterally grooved and well exposed in most (but see p. 81 under *C. nilsoni*), the second longer than the first; lower margin of caudal with subterminal notch; teeth one-cusped in both jaws, the lowers wider than the uppers, with cusp directed strongly outward all along each side of jaw, and with the bases of successive teeth overlapping outwardly; margins of upper teeth smooth; margins of lower teeth finely serrate in some species but smooth in others; the cusp of the median lower tooth either erect and symmetrical or oblique; upper teeth subtriangular, with the

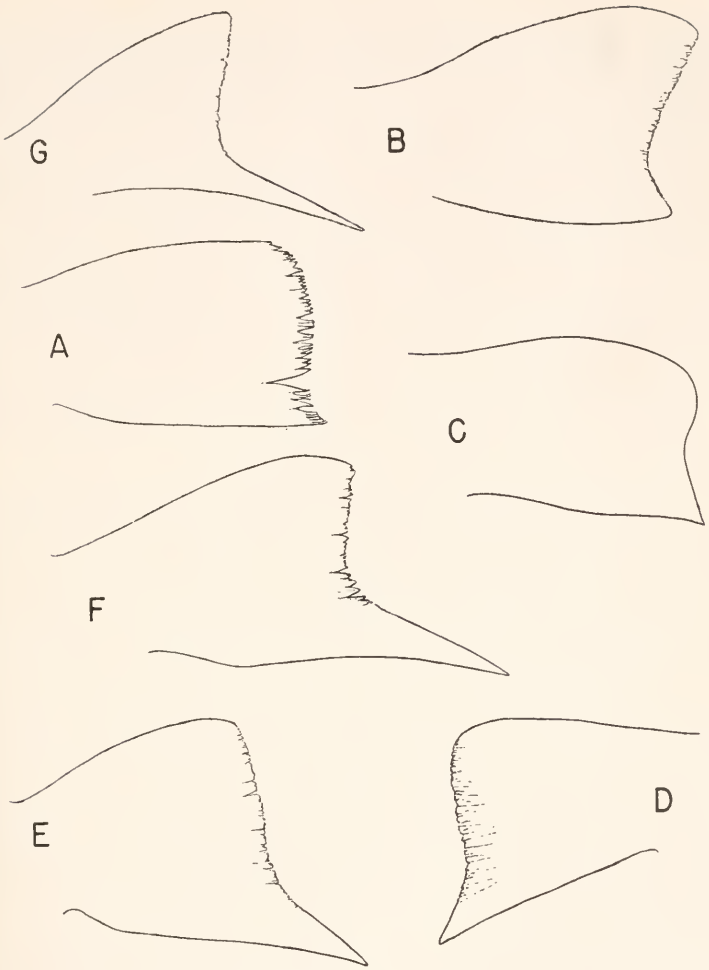

Fig. 8. Pectoral fin in different species of *Centrophorus*, adjusted to approximately equal lengths along outer margin, to show shape of inner posterior corner. A, *foliaceus*, same specimen as in Fig. 7F. B, *squamosus*, female, 1230 mm. long, southwest of Iceland. C, *steindachneri*, type specimen, after Pietschmann 1908, Pl. 1, Fig. 2B. D, *acus*, type specimen, male 820 mm. long, Japan, Mus. Comp. Zool. No. 1049. E, *uyato*, male, 429 mm. long, northern part of Gulf of Mexico, Mus. Comp. Zool. No. 38165. F, *granulosus*, female, 922 mm. long, northern part of Gulf of Mexico, U. S. Nat. Mus. No. 157833. G, *scalpratus*, Victoria, Australia, after McCulloch.

bases of successive teeth in contact along row, or slightly overlapping, the cusp erect and nearly symmetrical near center of mouth in most species, but nearly or quite as oblique as the lowers all along each side of jaw in a few species (p. 72); median upper tooth either symmetrical or oblique; inner corner of pectoral fins at least quadrate and angular, and more or less extended in most species (Fig. 8); snout to mouth in all known species, not longer than from mouth to level of origin of pectoral fins; nostrils without barbel; preoral clefts present, more or less expanded inwardly (Fig. 1B). Caudal peduncle without precaudal pits or lateral ridges; dermal denticles on sides of body low; block-like, scale-like, or conical in different species (Bigelow, Schroeder and Springer 1953, p. 270, fig. 3).

Maximum recorded lengths, 1500 mm. for **C. granulosus* and 1420 mm. for **C. squamosus* (Bocage and Capello 1866, pp. 26, 27).

Depth range. The only definite records of depths of capture that we have found are 631 meters for **foliaceus,* off Japan (Günther 1887, p. 5), and 1756 meters in Philippine waters (Smith and Radcliffe 1912, p. 679); 366-375 meters for **granulosus* (specimen in U. S. Nat. Mus. from Gulf of Mexico); 50-400 meters for **uyato* (Poll 1951, and specimens we have seen from Gulf of Mexico); "common between about 400 and 1500 meters" for **squamosus* (Grey 1956, p. 96) with one record from 1875 meters; 400 meters for *machiquensis* (Maul 1955, p. 5; and 128 to 439 meters for *scalpratus* (Whitley 1940, p. 145). While no definite information is available for any one of the group of additional species described from Japan (**acus,* **atromarginatus,* **tesselatus,* and *steindachneri*), it seems that their normal ranges are restricted to depths greater than 100-200 meters.

Remarks. The most distinctive single character of the genus (though probably not one of any great phylogenetic importance) is the angular and usually more or less extended inner corner of the pectoral fins. The range in this respect (Fig. 8) may be illustrated by **C. foliaccus* Günther 1877 of Japan, in which the pectoral inner corner is only very slightly extended or even rectangular, through conditions in **squamosus* Bonnaterre 1788, in **acus* Garman 1906 (incl. *steindachneri* Pietschmann 1907), in **uyato* Rafinesque 1810, and in *harrisonii* McCulloch 1915,

where it is extended somewhat more, and in **granulosus* Bloch and Schneider 1801, where it is still further prolonged, as it also is in *scalpratus* McCulloch 1915.

The gradation, in short, in the shape of the pectoral, is so nearly unbroken that the revival of *Lepidorhinus* Bonaparte 1838 by Garman (1913, p. 211) and of *Entoxychirus* Gill 1862 by Fowler (1941, p. 242), based on differences in this regard, serves no useful purpose, whether from the practical standpoint, or as representative of probable phylogenetic relationship. In the type specimens, in fact, of *C. nilsoni* from New Zealand (Thompson 1930, p. 277), and of **C. tesselatus* from Japan (now in the Museum of Comparative Zoology; Fig. 10 C, D), the inner corner of one of the pectoral fins is extended, but not that of the other pectoral (apparently undamaged).

Teeth. The cutting edge of the lower teeth of **C. granulosus* is described and pictured both by Müller and Henle (1841, p. 89, Pl. 33) and by Bocage and Capello (1866, p. 26, Pl. 1, fig. 3D) as finely serrate. Similarly, the reserve rows (5 in number) of our eastern Atlantic specimen of this species are finely but irregularly serrate in some places (Fig. 9A), though not in others. The lowers in the more anterior of the two rows that are visible from outside the mouth (no longer in function) also show faint traces of serration here and there. But the lowers in the functional row are slightly jagged in places, at most. And the situation is essentially similar in the case of a Gulf of Mexico specimen of **granulosus,* on which some of the lowers show microscopically fine serration, but others are merely somewhat irregular in outline, probably as the result of wear. (For further details, see Bigelow, Schroeder and Springer 1955, p. 6, Fig. 2C, p. 8). Bocage and Capello (1866, Pl. 1, Fig. 3E) picture the upper teeth of **granulosus* as finely serrate, like the lowers. But this seems to have been an error on the part of the artist, for the uppers are smooth on both of the specimens of **granulosus* that we have examined — also on all the specimens of other species of the genus that we have studied, for that matter.

In **C. squamosus,* as represented by a female about 1250 mm. long from Iceland (Fig. 10A), and by jaws of a somewhat larger individual, presumably from near the Faroes (Fig. 11B), the lowers in the outermost of the two rows that are visible from

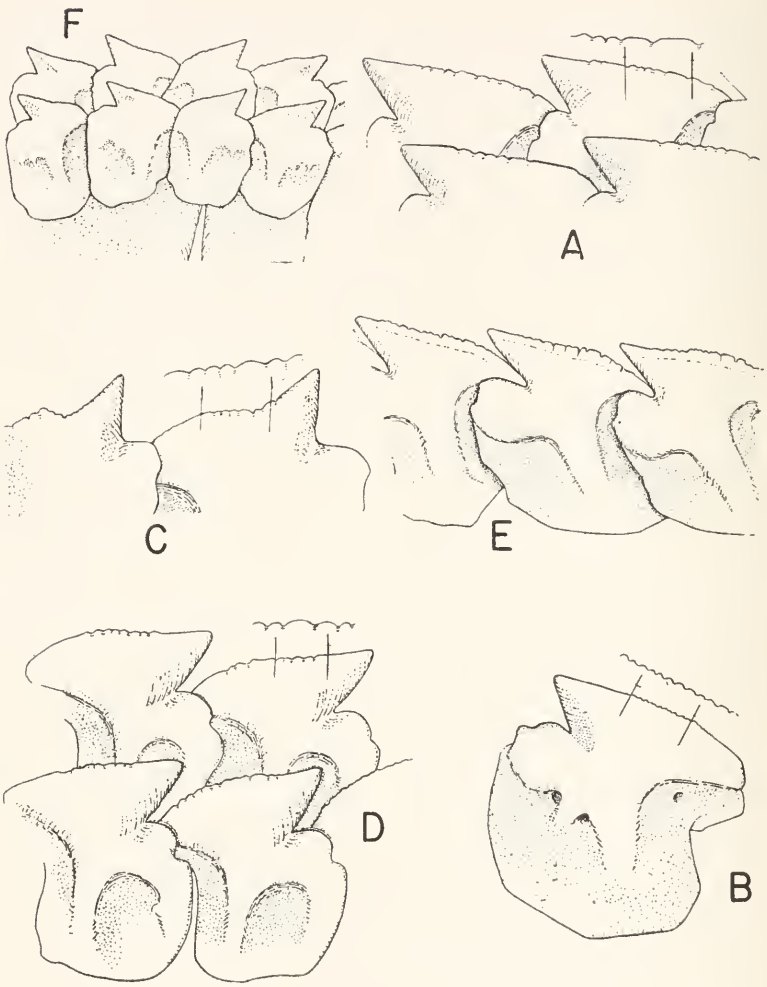

FIGURE 9

outside the mouth are finely serrate along the central part of the cutting edge, those in the reserve rows less clearly so. The lowers in the first reserve row (the edges of the functional rows are badly worn) are also unmistakably though faintly serrate in places (Fig. 9C) on the type specimen of **tesselatus*. On the type specimen of **atromarginatus* (on which the teeth are in better condition), the lowers (Fig. 9D) are irregularly but unmistakably serrate. They are described as "serrated" in *scalpratus* (McCulloch 1915, p. 98) from Australia also. And the two rows of lower teeth that are visible from outside the mouth in the type specimen of the Japanese **acus* Garman 1906 show faint and irregular traces of microscopically fine serration here and there, though not so distinctly as these appear on Garman's (1913, Pl. 12, fig. 6) illustration when the latter is viewed under a lens. In the Australian *harrisonii*, also, the edges of the lower teeth are irregularly serrate (Fig. 9E). On the other hand, we have not detected any trace of marginal serration either on the lower teeth of a juvenile male *foliaceus*, 351 mm. long, from Japan (Fig. 7G), or on those of *uyato*, whether on a 429 mm. male from the Gulf of Mexico (Bigelow, Schroeder and Springer 1953, p. 271, fig. 4) or on a 480 mm. male from the Mediterranean. Thus the presence or absence of serrations on the cutting edge of the lower teeth seems not to be a useful basis for generic separation here, though it has long been so regarded among the carcharhinid sharks.

Similarly, the degree of obliquity of the upper teeth ranges

Fig. 9. Lower teeth in different species of *Centrophorus* to show the degree of marginal serration. A, *granulosus*, male, about 855 mm. long, eastern Atlantic, Mus. Comp. Zool. No. 662, 2nd and 3rd reserve rows, x about 9. B, *squamosus*, third tooth, outermost row, from jaw of specimen taken near the Faroes, Mus. Comp. Zool. No. 39571, x about 5.5. C, *tesselatus*, male, 887 mm. long, type specimen, Mus. Comp. Zool. No. 1031, Japan, first row visible from outside the mouth, x about 15. D, *atromarginatus*, female about 870 mm. long, type specimen, Japan, Mus. Comp. Zool. No. 1455, first two rows visible from outside the mouth, x about 8. E, *harrisonii*, Australia, teeth from one of McCulloch's original specimens, made available to us through the kindness of Dr. G. P. Whitley, x about 10. F, *squamosus*, lower teeth at center of jaw of same specimen as in B, to show the obliquity of the median tooth, x about 2.4.

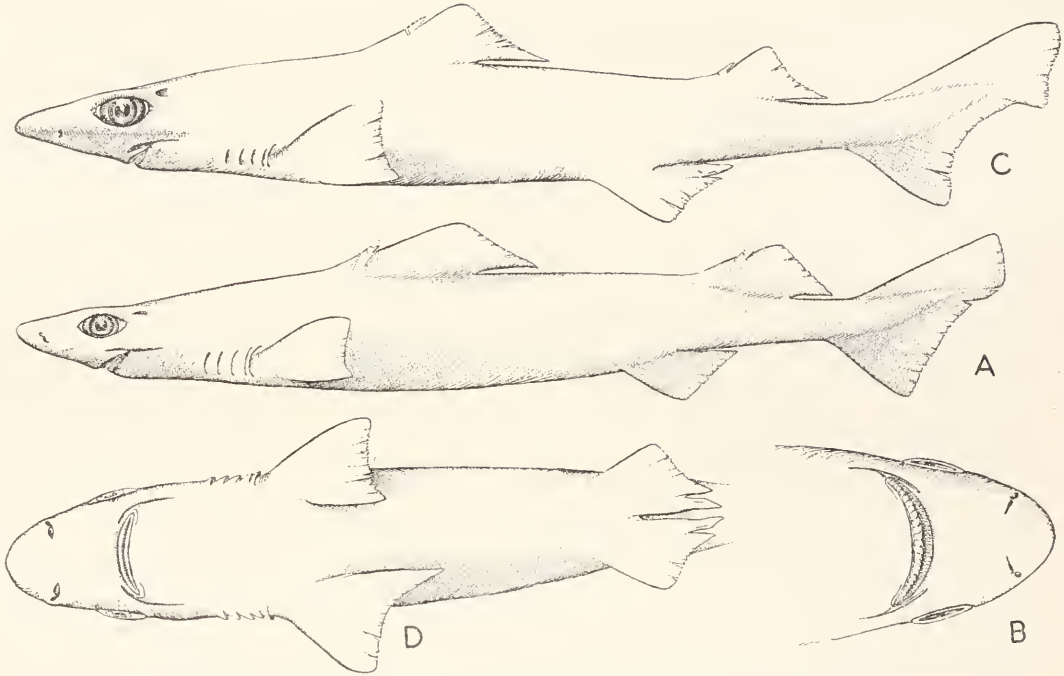

Fig. 10. A, *Centrophorus squamosus*, female, 1250 mm. long from southwest of Iceland. B, ventral view of head of same. C, *Centrophorus tesselatus*, male, 887 mm. long, type specimen, Mus. Comp. Zool. No. 1031, Japan. D, ventral view of anterior part of trunk of same, to show the difference in shape between the two pectoral fins of this particular specimen.

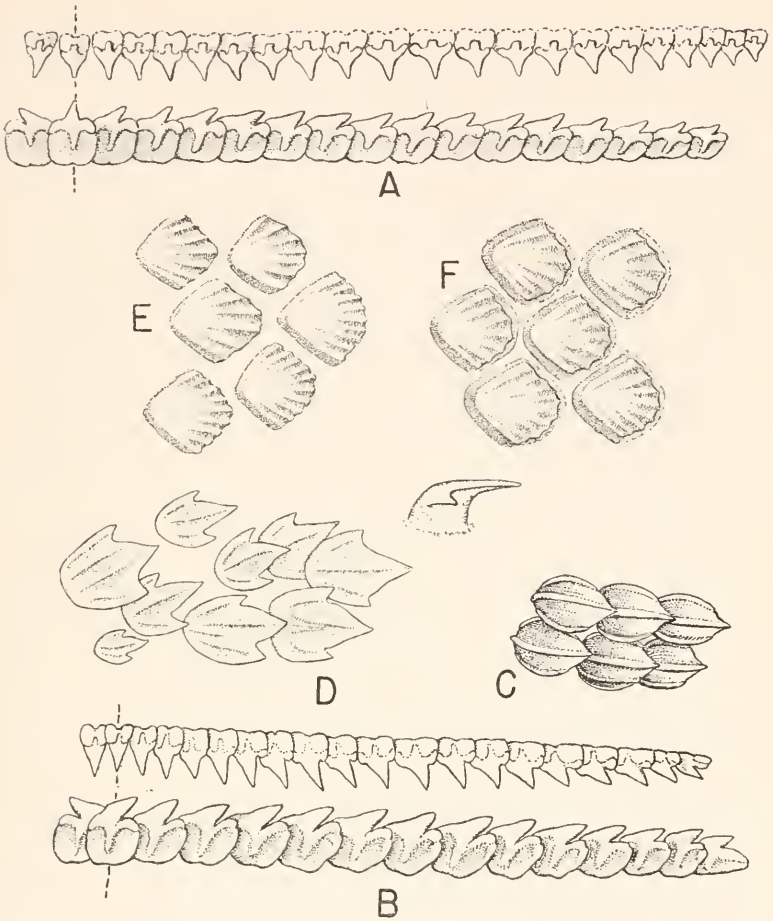

Fig. 11. A, *Centrophorus tesselatus,* same specimen as in Fig. 9C, upper and lower teeth, left hand side of mouth, x about 3. B, *Centrophorus squamosus,* female, about 1100 mm. long, from southwest of the Faroes, upper and lower teeth, left hand side of mouth, x about 1.3. C, *Centrophorus squamosus,* same specimen as in B, denticles from side below first dorsal fin, x about 5.5. D, *Centrophorus acus,* male, 810 mm. long, type specimen, Mus. Comp. Zool. No. 1049, Japan, denticles from side below first dorsal fin, x about 15. E, *Centrophorus atromarginatus,* female, about 850 mm. long, type specimen, Mus. Comp. Zool. No. 1455, denticles from side below first dorsal fin, x about 17. F, *Centrophorus tesselatus,* same specimen as in A, denticles from side, x about 17.

from the state in **granulosus* and in **atromarginatus* (Garman 1913, Pl. 13, fig. 2), where those along the central sector of the jaw are erect and symmetrical, or nearly so, to the state in **uyato* (Bigelow, Schroeder and Springer 1953, p. 271, fig. 4) and in *harrisonii* (McCulloch 1915, p. 99, Pl. 14, fig. 3), where this is true only of the first few teeth next to the midpoint of the jaw, the teeth farther out along the latter being nearly or quite as strongly oblique as the lower teeth are.

As remarked above (p. 21), the specimen on which Johnson (1867) based his new genus and species *Machephilus dumerili*, but which Vaillant (1888, p. 70), Garman (1913, p. 212), Rey (1928, p. 440), and Bigelow, Schroeder and Springer (1953, p. 224) have considered as identical with **Centrophorus squamosus* (Bonnaterre) 1788, had a symmetrical tooth at the center of the lower jaw. Accordingly Vaillant (1888, p. 70), followed by Rey (1928, p. 443), included the presence or absence of a symmetrical median lower tooth as alternative between two varieties of **squamosus*. Conditions in this respect among specimens of *Centrophorus* that we have examined are as follows: **granulosus* (male about 855 mm. long, Europe, and female 922 mm., Gulf of Mexico); **squamosus* (2 females about 1250 and 1280 mm. long from Iceland and jaws of 4 somewhat larger specimens, probably from west of the Faroes, Fig. 11B); **acus* (type specimen, male about 820 mm., Japan); **atromarginatus* (type specimen, 857 mm., Japan); and **foliaceus* (male, 351 mm. long, Japan), the cusp of the median lower tooth is about as oblique as the cusps of the successive teeth outward, in each of the rows that are visible from outside the mouth. On the other hand, the cusp of the median lower tooth is erect and symmetrical in both these rows on the type specimen of **C. tesselatus* from Japan (Fig. 11A). And the two specimens we have seen of **C. uyato* are intermediate between these two extremes, the cusp of the median lower tooth being strongly oblique on a male of 480 mm. from Nice, France, but only very weakly so, as well as smaller than that of the succeeding teeth on another male of 445 mm. from the Gulf of Mexico (Bigelow, Schroeder and Springer 1953, p. 271, fig. 4). Evidently the degree of obliquity of the cusp of the median lower tooth is not an appropriate basis for generic separation here.

Dermal denticles. In some members of the genus the denticles

on the sides of the trunk are scale-like and overlapping, the rear edges even or tridentate, and with the ridges on the outer surface either parallel or diverging slightly rearward. In other species the denticles are more block-like or conical-thorn-like, not overlapping, more or less pointed, with the ridges converging rearward. And Rey's (1928, p. 239, fig. 143) account of the denticles of **C. granulosus* as more pointed on juvenile specimens than on adults seems actually to have been based on a specimen of **C. uyato* (Rey 1928, Pl. 3, fig. 2), a species for which pointed denticles are diagnostic. The shape of the denticles, indeed, is the most obvious character among those likely to serve as alternative in this genus as between groups of species. But to subdivide *Centrophorus* generically on this basis, or by the other minor characters on which Whitley (1940, pp. 145, 146) based his subgenera *Gaboa* (type *Centrophorus harrisonii* McCulloch 1915) and *Somnispinax* (type *Centrophorus nilsoni* Thompson 1930), seems not to serve any useful purpose, the total number of species concerned being so small, and their resemblance, in general, being so close one to another.

Nomenclatural status of the type species. The original description by Bloch and Schneider (1801, p. 135) of their *Squalus granulosus* reads as follows: "Sq. bruneus cute granulosa, aculeis 2 robustis compressis, postice parum incu ruis, intus concavis, primo in initio pinnae dorsi, secundo in initio mesurae, pinnis brevibus, dorsali pectoralibus propinquiorae quam ventralibus remotissimis, mesura caudale vicina, foraminibus temporum remotis, lunatis."

Obviously this is not enough to place Bloch and Schneider's five-foot specimen, whether as to genus among the Squalinae, or as to species, for it does not mention either the shape of the pectoral fins or the nature of the teeth. It is therefore fortunate for the sake of nomenclatural stability that while Müller and Henle's (1841, p. 89, Pl. 33) description and illustrations of their **granulosus* were based on an alcoholic specimen from near Sicily, they did have, for comparison, a dried specimen in Berlin from Bloch's collection, probably the one on which Bloch and Schneider's 1801 account was based, for they mention only the one. Müller and Henle's identification of their "*granulosus*" with the "*granulosus*" of Bloch and Schneider 1801 is therefore to be accepted — unless re-examination of the

type specimen (if still in existence) should eventually prove otherwise. This, in turn, implies that Müller and Henle's very excellent description and illustrations take precedence over the several accounts by subsequent authors, as the underlying basis for the comparison of species within the genus *Centrophorus*.

Species. The following named species, listed in chronological order, fall in *Centrophorus* as defined above (p. 64): **Squalus squamosus* Bonnaterre 1788 eastern North Atlantic (Figs. 1B; 8B; 9B; 10A, B; 11B, C), including *Machephilus dumerili* Johnson 1867; **S. granulosus* Bloch and Schneider 1801 including *Centrophorus braganzae* Regan 1906), type species, eastern North Atlantic (including the Mediterranean) and Gulf of Mexico; **Squalus uyato* Rafinesque 1810, eastern Atlantic (including the Mediterranean) and Gulf of Mexico (Fig. 8E); *Centrophorus moluccensis* Bleeker 1860, Amboina; *Centrophorus lusitanicus* Bocage and Capello 1864, coast of Portugal; **Centrophorus foliaceus* Günther 1877, Japan (Fig. 7F-I); **C. acus* Garman 1906, Japan (Fig. 11D); **C. tesselatus* Garman 1906, Japan (Figs. 9C, 10C, 11A); *C. steindachneri* Pietschmann 1907, Japan (Fig. 8C); **C. atromarginatus* Garman 1913, Japan (Figs. 9D, 11E); *C. harrisonii* McCulloch 1915, Australia (Fig. 9E); *C. scalpratus* McCulloch 1915, Australia (Fig. 8G); *C. nilsoni* Thompson 1930, New Zealand; and *C. machiquensis* Maul 1955, Madeira.

The specimen from southeastern Africa, described by Gilchrist (1922, p. 48) as *Atractophorus armatus,* is also provisionally referred here to *Centrophorus* (for discussion, see p. 82).

The members of the genus may be segregated by the shape of the denticles on the sides of the body, in three groups: A, denticles block-like, close set but not overlapping; B, denticles scale-like and overlapping more or less; C, denticles spur-like or conical-thorn-like and more widely spaced.

In the Atlantic, group A is represented by **C. granulosus,* by *lusitanicus* if this finally proves a distinct species (see below), and by the newly described *C. machiquensis,* which may prove to be identical with **granulosus* when a larger number of specimens of it have been examined; group B is represented by **squamosus;* group C by **uyato.* The distinctive features of **granulosus,* **squamosus* and **uyato* — all of which are fairly

well known now — are discussed elsewhere (Bigelow, Schroeder and Springer 1953, pp. 224-225; 1955, p. 7).

The status of *lusitanicus* remains uncertain. Originally described as distinct from **granulosus* by Bocage and Capello in 1864 but definitely classed by them in 1866 with **granulosus, lusitanicus* was revived as a separate species by Günther (1870, pp. 420-421), and was so regarded both by Regan (1908) and by Garman (1913, p. 199). Again relegated to the synonymy of **granulosus* by Rey (1928, p. 436), it has been revived by Nobre (1935, p. 449). And Mr. G. E. Maul informs us that the first dorsal fin of a specimen which he has examined in the British Museum is larger than in **granulosus*, as appears from the following tabulation.

Proportional dimensions, in per cent of total length, of (A) *Centrophorus lusitanicus*, male, 742 mm. long, coast of Portugal, based on data furnished to us by Mr. G. E. Maul from a specimen in the British Museum, and (B) **Centrophorus granulosus*, female, 922 mm. long, Gulf of Mexico (U. S. Nat. Mus., No. 157833).

	A	B
Snout length in front of mouth	9.4	9.1
First dorsal fin: vertical height	7.4	5.4
Base, from anterior origin of spine	11.7	8.5
Free rear margin of fin	7.3	6.9
Second dorsal fin: vertical height	6.1	5.0
Base, from anterior origin of spine	6.6	5.7
Free rear margin of fin	4.0	4.5
Caudal fin: length of upper margin	19.7	20.3
Distance from snout to: origin of first dorsal spine	32.1	34.8
origin of second dorsal spine	67.0	69.2
upper origin of caudal fin	80.3	79.7
origin of pectoral fins	22.2	22.2
origin of pelvic fins	60.7	58.7
Interspace between: origin of first dorsal spine and second dorsal spine	34.9	34.4
base of second dorsal and lower origin of caudal	6.6	6.0
Distance from: origin of pectorals to origin of pelvics	38.4	37.6
origin of pelvics to lower origin of caudal	15.8	18.1

Until a larger number of specimens have been measured to determine how wide the range of variation may be, it must

remain an open question whether *lusitanicus* deserves recognition as a species separate from *granulosus*.

The situation is not clear for the species of *Centrophorus* that are known from the northern Pacific (all of them from Japan). Among these, group A (with block-like denticles closely spaced in quincunx arrangement) is represented by **tesselatus* and by **atromarginatus*. The demarcation between these two seems clear cut, from our examination of the type specimens in the Museum of Comparative Zoology. Thus the interspace between the rear end of the base of the first dorsal fin and the point of emergence from the skin of the second dorsal spine is as long as from tip of snout to axils of pectorals in **atromarginatus*, but is only as long as from the snout to origin of pectorals in **tesselatus*. Also, the inner corner of the pectoral fins is extended somewhat farther, the second dorsal spine is noticeably longer, and the cusps of the lower teeth are not only more strongly oblique but their cutting edge less deeply concave in **atromarginatus* than in **tesselatus*. Furthermore, the cusp of the median lower tooth, which is strongly oblique on the type specimen of **atromarginatus*, is erect and symmetrical on the type specimen of **tesselatus*, as noted above (p. 72). But this last difference may be a sexual one.

It remains an open question whether **atromarginatus* is separable from **granulosus* of the Atlantic. At least, our comparison of the type specimen of the former (a female of 850 mm.) with a male **granulosus* of 860 mm. from the eastern Atlantic, with a female of that species, 922 mm. long from the Gulf of Mexico (Bigelow, Schroeder and Springer 1955, fig. 2), and with Müller and Henle's (1841, Pl. 33) excellent picture of a **granulosus* from the Mediterranean, has not revealed any differences that might seem of specific rank, unless it be that the gill openings are not as long in the Japanese form (third gill is about 64 per cent as long as distance between nostrils) as in our Gulf of Mexico specimen (third gill about 80 per cent as long as distance between nostrils). And while Garman (1913, p. 197) described the teeth of **atromarginatus* as "not serrate," the lowers of the type specimen do show traces of fine serrations along the cutting edge (Fig. 9D) much as in the case of **granulosus* (Fig. 9A), in **tesselatus* also, for that matter (Fig. 9C). Pietschmann (1908, p. 663), in fact, has reported under

the name *granulosus* two Japanese specimens of *Centrophorus,* respectively 536 mm. and 908 mm. long, that he had compared with two *granulosus* of corresponding sizes from the Mediterranean. But the actual identity of his Japanese specimens calls for verification (if they are still in existence) for their denticles are described (Pietschmann 1908, pp. 663-667) as differing in shape from those of **granulosus* of the Atlantic. Pietschmann also united both **tesselatus* and **acus* Garman with **granulosus.* But as implied in the foregoing discussion, **tesselatus* differs from **atromarginatus.* And the denticles on the sides of the body of **acus* (no figures of which had appeared when Pietschmann wrote) differ widely from those of **granulosus,* for they are scale-like, with tridentate rear margins (Fig. 11D).

The **granulosus-*tesselatus-*atromarginatus* group of the Northern Hemisphere has a close ally in the Southern Hemisphere of the Pacific in *scalpratus* of Australian waters, except that McCulloch's (1915, Pl. 13, figs. 2-7) illustrations show the denticles on its sides as more pointed than those of **granulosus* of the Atlantic and Gulf of Mexico (Bigelow, Schroeder and Springer 1953, p. 270, fig. 3A; 1955, fig. 2D), or of the Japanese representative of the latter (p. 76). Other differences suggested by McCulloch's illustrations of *scalpratus* may be due to different methods of measurement, etc. The embryo from Amboina that was described by Bleeker in 1860 as *C. moluccensis* appears also to fall in this same group, for Regan (1908, p. 51), who saw the type specimen, located it in the subsection of the genus with "posterior angle of pectoral fin considerably produced and acutely pointed." And the little else that is known of its fins and bodily dimensions is consistent with this. But the shape of its denticles is not known.

Group B, with scale-like denticles (p. 74), is represented in the northwestern Pacific by **foliaceus,* originally described from Japan, and reported by name (with very brief comment) from deep water (960 fathoms) among the Philippines (Smith and Radcliffe 1912, p. 679); by **acus* from Japan; and by *steindachneri,* also from Japan. Among these, *steindachneri,* with tridentate flank denticles and with the inner corner of the pectorals only slightly extended (Fig. 8C; Pietschmann 1908, p. 676, text fig. 3; Pl. 1, fig. 1) agrees so closely with the type specimen of **C. acus* as to make it reasonably certain that the two represent

but a single species, to be named *acus* on the ground of priority. **Acus,* in turn, is allied to **foliaceus.* But it differs from the latter in the evident extension of the inner corner of its pectoral fins, for these are not appreciably extended in **foliaceus,* either as they are represented by Günther (1887, p. 5, Pl. 2, fig. A), or as they appear on two immature males of **foliaceus,* respectively 325 and 350 mm. long, from Japan (U. S. Nat. Mus., Nos. 161517 and 161518) that we have examined (Fig. 7F). The dermal denticles, also, on the sides of the type specimen of **acus* differ conspicuously from those of **foliaceus,* for while they are tridentate in both cases, they are not only broader, relatively, with shorter marginal teeth and less regularly overlapping in **acus* (Fig. 11D) than in **foliaceus* (Fig. 7H), but so much smaller relatively that the one species is separable from the other at a glance by this character alone. **C. foliaceus,* indeed, is by far the roughest-skinned species of *Centrophorus* that we have seen. **Acus* is also firmer-bodied than **foliaceus,* at least in the preserved state, and it is of a paler hue below than above, whereas the specimens of **foliaceus* we have seen are of as dark a chocolate brown below as above. The species **acus* may, therefore, be retained as distinct, at least until someone re-examines the type specimen of **foliaceus,* now in the British Museum. (For an account of **acus,* with beautiful illustrations, see Garman 1913, p. 199, Pl. 12, figs. 5-8.)

The accounts of **foliaceus* by Günther (1887, p. 5) and by Jordan and Fowler (1903, p. 631), do not especially emphasize the characters now known to be diagnostic of species within the genus *Centrophorus.* A more detailed account from this point of view, with measurements, is therefore included here (p. 78).

Centrophorus foliaceus Günther 1877

Figure 7F-I

Study material. Immature male, 351 mm. long, U. S. Nat. Mus. No. 161518, Okinosa, Japan.

Proportional dimensions of specimen listed above, in per cent of total length.

Snout, length in front of: outer ends of nostrils 3.4; mouth 10.8.
Eye: length, 4.8.
Mouth: breadth, 7.6.

Nostrils: distance between inner ends, 4.0.

Gill opening lengths: First, 2.1; second, 2.4; third, 2.4; fourth, 2.4; fifth 2.0.

First dorsal fin: vertical height, 5.0; length from imbedded base of spine to rear end of base of fin, 9.0.

Second dorsal fin: vertical height, 5.0; length from imbedded base of spine to rear end of base of fin, 8.0.

Caudal fin: upper margin, 21.1; lower anterior margin, 15.7.

Pectoral fin: outer margin, 10.8; inner margin, 7.7; width, 7.3.

Distance from snout to: imbedded base of first dorsal spine, 36.2; imbedded base of second dorsal spine, 65.5; upper origin of caudal, 78.9; origin of pectorals, 25.4.

Interspace between: rear end of base of first dorsal and imbedded base of second dorsal spine, 22.5; rear end of base of second dorsal and upper origin of caudal, 5.7; base of pelvics and lower origin of caudal, 12.4.

Distance from origin to origin of: pectorals and pelvics, 33.7; pelvics and caudal, 17.6.

Teeth: $\frac{16\text{-}1\text{-}16}{14\text{-}14}$

Head, to origin of pectorals, about ⅓ of trunk to upper origin of caudal fin; snout in front of mouth about 42 per cent of head to pectorals; eye about 19 per cent as long as head; distance from tip of snout to front of eye about 29 per cent of head; distance between inner ends of nostrils about 37 per cent as long as snout to mouth; longest gill openings (2nd, 3rd and 4th) about half as long as eye; mouth transverse, scarcely arched; distance between inner ends of preoral clefts about 1.75 times as great as between nostrils.

Upper teeth short, triangular, the median tooth erect, symmetrical, but the subsequent teeth increasingly oblique outward along the jaw, with the inner edges of those toward the corners of the mouth nearly horizontal; the lowers wider than the uppers, the cusps directed so sharply outward as to form a nearly unbroken cutting edge paralleling either side of the jaw. Cutting edge of lowers perfectly smooth, both in the reserve rows and in the outermost of the two rows visible from outside the mouth; the 2nd row slightly irregular, but not definitely serrate. The condition of the specimen does not allow us to determine whether or not there was a symmetrical median tooth in the lower jaw.

Dermal denticles scale-like, close set and largely overlapping, those on upper and lower sides of snout ovate, but those on body as a whole tridentate, lanceolate in general form, with the median tooth much the longest, on short pedicle, rising steeply from the skin and with high median crest; those on back, anterior to first dorsal spine, the largest. Length of first dorsal fin, measured from anterior side of imbedded origin of spine about 2.5 times as long as distance between nostrils; interspace between rear end of base of first dorsal fin and anterior edge of imbedded base of second dorsal spine about as long as from tip of snout to second gill openings. Second dorsal fin similar in shape to first dorsal, about 90 per cent as long, basally, as first, similarly measured (see above). Dorsal spines both well exposed; exposed portion of second about 1.5 times as long as that of first; distance between first and second spines, at points of emergence from the skin, about 1.5 times as long as from tip of snout to first gill openings. Interspace between rear end of base of second dorsal fin and origin of upper side of caudal about as long as from point of emergence from skin of second dorsal spine to rear end of base of second dorsal fin. Caudal fin about 20 per cent of total length, of the shape shown in Figure 7F. Distance from origin of lower side of caudal to rear end of bases of pelvics about as long as from rear edge of eye to origin of pectoral fins. Rear tips of pelvics (when laid back) about in a line with point of emergence from skin of second dorsal spine; origin of pelvics anterior to imbedded base of second dorsal spine by a distance about as long as from rear end of eye to first gill openings. Pectorals with outer margin about as long as from eye to fourth gill openings; outer corner broadly rounded; distal margin weakly sinuous, reaching, when laid back, about even with imbedded base of first dorsal spine; inner corner angular, with a few of the horny rays slightly extended (Fig. 8A).

Color. Plain dark brownish gray above and below; the rear margins of pectorals and tip of dorsals pale edged, after many years in alcohol.

Remarks. **C. foliaceus* is recognizable at a glance, so widely does its dermal armature, with close-set, strongly tridentate, high-crested denticles, rising steeply from the skin, differ from that of every other *Centrophorus* that we have seen, or that has

been pictured. Other distinctive characters for it (within the genus *Centrophorus*) are: the shape of the inner corner of its pectoral fins (p. 66), the lack of any abrupt transition from the general contour of its back to the rising slope of the first dorsal fin, and the pronounced obliquity of its teeth, uppers as well as lowers, as described above (p. 79).

In all these respects the specimen here described agrees with Günther's (1887, p. 5, Pl. 2, fig. A) account of a 470 mm. (18½ inch) male, except that its inner pectoral corner is very slightly extended ("rectangular, not produced" according to Günther), and that it is only the median upper tooth that is erect in the upper jaw, the lateral upper teeth being strongly oblique (see above), whereas Günther characterized "the anterior teeth of the upper jaw" as erect, the laterals as "slightly oblique." These slight differences do not seem to call for recognition in nomenclature on the basis of so few specimens.

The Japanese **foliaceus* resembles **squamosus* of the eastern North Atlantic in its bodily proportions in general, in the relative locations of its fins, and in the scale-like nature of the denticles on the sides of its trunk. But it differs from **squamosus* in the quadrate outline of the inner corner of its pectoral fins (definitely though only slightly extended in **squamosus* cf. Fig. 8A with Fig. 8B), and in the narrower, more regularly tridentate and more steeply elevated denticles (cf. Fig. 7H with Fig. 11C), so that the two species clearly are separable, the one from the other.

The Northern Hemisphere species with scale-like denticles are represented in the Southern Hemisphere by *nilsoni* of New Zealand (Thompson 1930, p. 277, Pl. 44). *Nilsoni* falls close to **acus* in the shapes of the inner corner of its pectoral fins and of the denticles on the sides of its trunk. But its fin-spines are described by Thompson (1930, p. 277) as "low and largely covered," a character which (if normal) sets it apart.

The North Atlantic **uyato,* with conical-thorn-like denticles on its sides and with the inner pectoral corner moderately extended, is similarly replaced in the South Pacific by *harrisonii* of Australian waters. Going back a step further in shark history, the embryo reported from Port Jackson, Australia, many years ago by Steindachner (1867, p. 333) under the name *Acanthias uyato* Rafinesque, may have been the first specimen

of *harrisonii* to come under scientific observation. On the other hand, Whitley (1934, p. 199) has suggested that it may have been a *Squalus*, a view supported by Steindachner's description of it as marked with large white spots on its back. However this may be, the cutting edge of the lower teeth, which are smooth in the Atlantic **uyato* (p. 69), are irregularly serrate (Fig. 9E) in *harrisonii* (described as imperfectly so by McCulloch 1915, p. 99). And other differences between the Atlantic and Indo-Pacific populations may come to light when adequate series of specimens from the two ocean areas have been compared.

Finally, we face the case of *Atractophorus armatus* from the Natal coast of southern Africa, the type specimen of which seems to have been a typical *Centrophorus* in all respects, except that the tip of its second dorsal fin spine was described and pictured as "barbed, like an arrowhead" (Gilchrist 1922, p. 48, Pl. 7, fig. 3). Unfortunately, the type specimen of *armatus* is no longer to be found.[11] But the collection of the Government Marine Survey of South Africa does contain a juvenile shark, 330 mm. long, apparently an *armatus*, the second dorsal fin spine of which (while not two-barbed) bears a single, wing-like expansion on its rear side, close to its tip (Fig. 7J). And any conformation of the spine tip, other than tapering to a point (if normal) makes *armatus* unique among known sharks, whether modern or fossil. We may either accept this feature as justifying the generic separation of *Atractophorus* from its parent genus *Centrophorus*, or we may transfer *armatus* to *Centrophorus*, as the genus in which it would fall on the basis of ancestral relationship, were it not for the single character in question. We choose this last alternative, partly because we see no useful purpose to be served in acting otherwise; partly because this choice seems the more likely of the two to focus attention on *armatus* when additional specimens come to hand; and partly because of the chance that the peculiar conformation of the second dorsal spine tip on the two specimens that have been examined may have represented an abnormality, or may have been the result of accidental damage.

If *armatus* is, in fact, a *Centrophorus*, its closest relationship is with *harrisonii*, with which — and with **uyato* of the North

[11] We are so informed by Prof. J. L. B. Smith, who has made a special search for it in the collection of the Government Marine Survey of South Africa.

Atlantic — it shares pectoral fins with extended inner corner (but shorter from origin to rear tip than from tip of snout to level of first gill openings), and denticles on sides of body that are described as acuminate, with many sharp ridges (Gilchrist 1922, p. 49).

Key to species of *Centrophorus*

1. Denticles on sides of trunk scale-like, overlapping, the ridges on their outer surface (if more than one) parallel or diverging slightly rearward 2
   Denticles on sides of trunk block-like or conical-thorn-like, not overlapping; the ridges on their outer surface converging rearward, if at all 5
2. Denticles on sides of body not definitely tridentate (Fig. 11C) ..... **squamosus* Bonnaterre 1788. Northeastern Atlantic. p. 74
   Denticles on sides of body regularly tridentate (Figs. 7H, 11D) 3
3. Inner corner of pectoral fins quadrate, not appreciably extended (Fig. 8A); dermal denticles on sides of body as in Figure 7H ..... **foliaceus* Günther 1877. Japan; also reported by name from the Philippines (Smith and Radcliffe 1912, p. 679), and from New Zealand (Richardson 1956, p. 7). p. 78
   Inner corner of pectoral fins definitely extended, though not greatly so (Fig. 8D); denticles on sides of body as in Figure 11D) 4
4. Both of the dorsal fin spines prominent and well exposed ..... *acus* Garman 1906, Japan. p. 77
   Both of the dorsal fin spines low and largely covered ..... *nilsoni* Thompson 1930, New Zealand; p. 81
5. Pectoral fin, from origin to inner rear corner, about as long as from tip of snout to level of fourth gill openings ..... *scalpratus* McCulloch 1915, Australia. p. 74
   Pectoral fin from origin to inner rear corner shorter than from tip of snout to level of first gill openings 6
6. Denticles on sides of trunk block-like, quadrate, closely spaced in quincunx arrangement; upper teeth erect and symmetrical, or nearly so, all along central part of jaw 7
   Denticles on sides of trunk conical-thorn shaped, loosely spaced in random arrangement; upper teeth strongly oblique, except for the first few next to the mid-point of the jaw, which are erect 8
7. Distance from rear end of base of first dorsal fin to point of emergence

from the skin of second dorsal spine is as long as from tip of snout to axil of pectorals; exposed part of second dorsal fin spine is about 75 per cent as long as distance between nostrils .....
granulosus Bloch and Schneider 1801 (including *lusitanicus* Bocage and Capello 1864); Mediterranean with neighboring eastern Atlantic, Gulf of Mexico, p. 73; and reported by name from tropical West Africa (Cadenat 1950, p. 101); also *machiquensis* Maul 1955, Madeira (p. 74); and *atromarginatus* Garman 1913, Japan (see discussion, pp. 76-77).

Distance from rear end of base of first dorsal fin to point of emergence from the skin of second dorsal fin spine is only about as long as from tip of snout to origin of pectorals; exposed part of second dorsal spine only about 40 per cent as long as distance between nostrils .....
tesselatus Garman 1906, Japan. p. 74

8. Cutting edges of lower teeth smooth .....*uyato* Rafinesque 1810. Mediterranean, eastern tropical Atlantic along the African coast from Senegambia (Rochebrune 1883-1885, p. 24) to Lat. about 20° S (Poll 1951, p. 65); also Gulf of Mexico. p. 74

Cutting edges of lower teeth irregularly serrate (Fig. 9E) ..*harrisonii* McCulloch 1915. Australia. p. 74

Position uncertain: *moluccensis* Bleeker 1860, Amboina; also *armatus* Gilchrist 1922, southeastern Africa (p. 82).

Genus CENTROSCYMNUS Bocage and Capello 1864

Centroscymnus Bocage and Capello 1864, p. 263; 1866, p. 29; type species **C. coelolepis* Bocage and Capello, off Portugal.

Generic Synonyms:

Centrophorus in part, Günther 1870, p. 423, for *C. coelolepis* Günther, equals **Centroscymnus coelolepis* Bocage and Capello 1864; Thompson 1930, p. 277, for *C. waitei* Thompson, New Zealand.

Centroselachus Garman 1913, p. 206, type species **Centrophorus crepidater* Bocage and Capello 1864, off Portugal.

Proscymnodon (subgenus) Fowler 1934, p. 239, type and only included species *Centrophorus plunketi* Waite 1909, New Zealand.

Scymnodon in part, Fowler 1941, p. 225, for *Centrophorus plunketi* Waite 1909, New Zealand.

Not *Scymnodon* Bigelow, Schroeder and Springer 1953, p. 230, for *Scymnodon melas* Bigelow, Schroeder and Springer 1953, p. 233, fig. 5, which is a young stage of *Centroscymnus coelolepis* (p. 100).

Generic characters. In general as in *Centrophorus* (p. 64), except with inner corner of pectoral fins broadly rounded (this is the most conspicuous difference between the two genera); the upper teeth more slender than the lowers, lancet shaped, those along central sector of mouth nearly as long as those midway out along either side of upper jaw; the successive teeth in the functional row not in contact basally, or hardly so; lower teeth smooth edged, the successive cusps directed so strongly outward as to form a nearly continuous cutting edge; median lower tooth not symmetrical; second dorsal fin spine, like first, either exposed more or less at tip, or entirely enclosed in the skin; dermal denticles on sides of body low, scale-like, with tridentate margins on young specimens in some species, and probably in all, also on adults in some species, but replaced later in growth in other species by denticles with evenly rounded margins and concave crowns; preoral clefts short in some species but so long in others as to leave only a narrow gap between their inner ends (see discussion, p. 87), considerably expanded inwardly in species where they are short (Fig. 1C) but not appreciably so in those where they are longest (Fig. 1D).

Maximum recorded length 1140 cm. for *C. coelolepis* (Bocage and Capello 1866, p. 31) and 1414 for *C. plunketi* (Waite 1910, p. 384).

Depth range. Centroscymnus coelolepis (p. 88), the shoalest record for which has been 329 meters, has its center of distribution between 400 meters and 2000 meters according to locality, and has been taken down to about 2700 meters (maximum yet recorded for any shark). It may fairly be classed as the deepest living of modern sharks. (For further details see Bigelow and Schroeder 1948, p. 498, and Grey 1956, pp. 97-98.) Depth records for the other members of this genus are 270-920 meters for *crepidater* off Iceland (Saemundsson 1922, pp. 192, 196, as *Centrophorus jonsonii*); 220 meters for *plunketi* (Waite 1910, p. 384); 780 meters for *rossi* (Alcock 1898, p. 144); and 512 meters for *fuscus* (Gilchrist and von Bonde 1924, p. 3).

Remarks. Teeth. The only characters mentioned by Bocage and Capello (1864, p. 263; 1866, pp. 19-20, 24, 29) in their successive generic diagnoses of *Centroscymnus* that contrast with their diagnosis for *Centrophorus* (1866, pp. 19, 22) were that the upper teeth of the former are awl-shaped and loosely spaced ("subuliformes écartés") and that its first dorsal fin spine is almost entirely enveloped by the skin. But a much more conspicuous difference than either of these is the rounded inner corner of the pectorals of *Centroscymnus,* as contrasted with their angular inner corner in *Centrophorus* (p. 66). Similarly, the only alternative character in their original diagnosis of *Centroscymnus,* as contrasted with *Scymnodon,* is the shape of the lower teeth, which Bocage and Capello characterized for the former as not unlike those of *Centrophorus* (i.e. as oblique, without symmetrical median tooth), but for *Scymnodon* as with symmetrical median tooth, the first tooth outward from it on either side erect, the succeeding teeth as increasingly oblique toward corners of mouth ("dens medianus impar, post eum dantes premum erecti, deinde versus angulum oris magis ac magis decumbentes," Bocage and Capello 1864, p. 263). But a second difference between the type species of *Centroscymnus* (**coelolepis* Bocage and Capello 1864) and of *Scymnodon* (**ringens* Bocage and Capello 1864), equally diagnostic and much more conspicuous, is that while the upper teeth along the central sector of the mouth are nearly as long as those midway out along each side of the jaw in *Centroscymnus,* they are much shorter than those midway along the jaw in *Scymnodon.* The value of this feature as a diagnostic character seems first to have been realized by Rey (1928, p. 486, fig. 152).

Dermal denticles. In the adults of some species (*plunketi* Waite 1910, New Zealand; **crepidater* Bocage and Capello 1864, eastern Atlantic) that are referable to *Centroscymnus* by their dentition, the denticles on the sides of the trunk are tridentate in outline, the outer surface sculptured with longitudinal ridges. In the adults of others (**coelolepis* Bocage and Capello 1864, both sides of the North Atlantic; *cryptacanthus* Regan 1906, Madeira; **owstoni* Garman 1913, Japan), they are rounded in outline, with smooth, concave crowns; also in *fuscus* Gilchrist and von Bonde 1924, southern Africa, so far as the concavity

of the crowns is concerned.[12] But it has been found by Tortonese (1952, p. 386, corroborated by Bigelow and Schroeder 1954, p. 47) that the rounded denticles of the adult **coelolepis,* and apparently those of **owstoni* as well (Bigelow and Schroeder 1954, p. 50), are preceded at early stages in growth (as proven by embryos of known parentage) by tridentate forms, the replacement of denticles of the juvenile shape by others of the adult shape taking place when a given specimen is half to two-thirds grown. For further details we refer the reader to our earlier account (Bigelow and Schroeder 1954, p. 47, fig. 2). It follows from this that our earlier acceptance of the shape of the denticles (Bigelow and Schroeder 1948, p. 451, following Garman 1913, p. 189) as alternative between *Centroscymnus,* where they are rounded on the type species at maturity (**coelolepis* Bocage and Capello 1864) and *Scymnodon,* where they are tridentate at maturity, is no longer tenable.

It seems appropriate here to recall that we owe to Steenstrup (1861) our knowledge that the dermal denticles of sharks do not persist throughout the life of the fish, growing as the latter grows, as the scales of bony fish do, but that they are constantly being shed, to be replaced by other, larger denticles. Thus several generations of denticles succeed one another during the life-span of any individual shark.

Fin spines. It seems worth emphasizing that the imbedded basal part of the fin spines is easily felt, in species in which their tips are concealed by the skin (p. 89).

Preoral clefts. The preoral clefts extend for about 40-50 per cent of the distance from the corner of the mouth toward the midline of the snout in **coelolepis* (incl. *cryptacanthus*) of the North Atlantic, in **owstoni* of Japan, and in *macracanthus* of the Magellanic region; about 60 per cent of that distance in *waitei* from New Zealand;[13] but for about 90 per cent of that distance in **crepidater* (incl. **jonsonii*) of the North Atlantic (Fig. 1D) and in *rossi* Alcock 1898 of the Indian Ocean (Alcock 1899, Pl. 26, fig. 3). Both **crepidater* and *rossi* fall, however, with the type species of *Centroscymnus* (**coelolepis*) in dental characters, in shape of pectoral fins, and in shortness of fin-

[12] The contour of the margins of the denticles is not known for *fuscus.*

[13] Taken from a drawing made available to us by Dr. J. A. F. Garrick before publication.

spines. Hence the difference in the length of the clefts does not call for generic recognition, especially where the total number of species concerned is so small.

Shape of caudal fin. Conditions in *Centroscymnus* argue against the presence or absence of a subterminal notch on the lower margin of the caudal as a subfamily alternative among the Squalidae, for while this notch is well marked in most of the members of the genus, it is indistinct in *waitei* (Garrick 1955, p. 233, fig. 1A). This seems the appropriate place for us to point out that the caudal of **coelolepis* is not correctly pictured in our earlier illustration (Bigelow and Schroeder 1948, fig. 94). Actually it is of the shape shown here on Figure 12 H.

Species. The following named species, listed in chronological order, are referable to *Centroscymnus* as defined here: **Centroscymnus coelolepis* Bocage and Capello 1864, type species, North Atlantic, east and west; **Centrophorus crepidater* (Bocage and Capello 1864), off Portugal; *Centrophorus rossi* Alcock 1898, Travancore Coast, India; *Centroscymnus cryptacanthus* Regan 1906, Madeira; *Centroscymnus macracanthus* Regan 1906, Magellanic region; **Centroscymnus owstoni* Garman 1906, Japan; *Centrophorus plunketi* (Waite) 1910, New Zealand (referred by Garman 1913, p. 210 and by Fowler 1941, p. 228 to *Scymnodon* because of its tridentate denticles); **Centrophorus jonsonii* (Saemundsson) 1922, Iceland; *Centroscymnus fuscus* Gilchrist and von Bonde 1924, southern Africa; *Centrophorus waitei* (Thompson) 1930, New Zealand.[14]

Detailed descriptions of the type species, **coelolepis*, with illustrations, have been given by Garman (1913, p. 204, Pl. 17, figs. 5-8), by Rey (1928, p. 451) and by Bigelow and Schroeder (1948, p. 494; 1954, p. 47). *Coelolepis* is known in the eastern Atlantic from the offing of Cape Verde and of Morocco to the Faroe Bank and to Iceland, including the western part of the Mediterranean; from the offing of Delaware Bay to the Banks of Newfoundland in the western. According to Regan's (1906, p. 437) account, his *cryptacanthus* from Madeira differs from the specimens of **coelolepis* that we have seen (including the one

[14] Our inclusion of *waitei* in *Centroscymnus* follows Garrick's (1955) study of the type specimen, the result of which was contributed to us by Dr. Garrick in advance of his publication.

on which Garman's illustration was based) in a slightly longer snout; in an interspace between the two dorsal fins about 6 times as long as the base of the first dorsal (4-5 times in *coelolepis*); in the extension rearward of the tips of the pelvic fins to abreast of the tip of the second dorsal fin; and in complete enclosure of the fin spines by the skin. Also, the denticles on the trunk rearward from abreast the first dorsal fin are described (Regan 1906, p. 437) as already rounded, and with concave crowns on a *cryptacanthus* only 700 mm. long (the type specimen), whereas various transitional stages are represented on a **coelolepis* of about that same size (690 mm., Bigelow and Schroeder 1954, p. 48, fig. 2). But with both **coelolepis* and *cryptacanthus* recorded from Madeira, the desirability is self-evident of comparison of the type of *cryptacanthus* (in the British Museum) with northern specimens of **coelolepis*.

**C. owstoni* from Japan (the type specimen of which is in the Museum of Comparative Zoology) differs from **coelolepis* of the Atlantic in a considerably longer snout, a somewhat larger eye, a considerably larger second dorsal fin relative to the size of the first dorsal, with the rear tip reaching more nearly to the upper origin of the caudal fin, and in relatively smaller — consequently more numerous — dermal denticles on the sides of the trunk.

The New Zealand shark that was described by Waite (1910) as *Centrophorus plunketi*, but which has been referred by Garman (1913 p. 210) to *Scymnodon*, and by Fowler (1933, p. 239; 1941, p. 228) to his subgenus *Proscymnodon*, is set apart from the *coelolepis-owstoni* pair by the tridentate shape of the denticles on the sides of the trunk on large specimens (type specimen a female 1414 mm. long) — presumably on small specimens also. And its denticles are both described and pictured (Waite 1910, p. 386, text fig.) as having as many as eight separate roots. The tips, also, of its pelvic fins are pictured (Waite 1909, Pl. 37) as reaching back only about as far as a perpendicular at the point of emergence of the second dorsal fin spine (they reach to a perpendicular at about the midpoint of the free lower margin of the second dorsal fin both in **coelolepis* and in **owstoni*), while the second dorsal fin is pictured as considerably larger in *plunketi* than it is either in **coelolepis* or in **owstoni*.

Dr. J. A. F. Garrick's study of the type specimen (a juvenile

male, 318 mm. long) of the shark described by Thompson (1930) as *Scymnodon waitei* places it definitely in the genus *Centroscymnus* as here defined, while his detailed account of it, with excellent illustrations, makes possible, for the first time, a satisfactory view of such of its characteristics as are the most evidently diagnostic of the species. Briefly, these are: snout in front of mouth shorter than distance from mouth to level of first gill openings; head, to origin of pectorals, about 20 per cent of total length; distance between inner ends of preoral clefts nearly or quite as long as between nostrils; base of second dorsal about twice (1.9) as long as base of first dorsal; dorsal fin spines with only the tips exposed; caudal fin without subterminal notch; dermal denticles on sides of body strongly tridentate, on four-angled base, and rising steeply from the skin; the outer exposed surface concave, without axial ridge; the denticles on the lower side of the snout ovate, with pointed tip and with prominent axial ridge. (For further details, including teeth, see Garrick 1955, pp. 233-238, figs. 1, 2.)

Thompson (1930, p. 278) followed by Richardson and Garrick (1953, p. 35) has suggested that *waitei* may prove to represent a stage in the growth of *Centroscymnus plunketi*, intermediate between the adult female that was the basis of Waite's original (1910) account of the latter, and the embryo, 165 mm. long, that was pictured subsequently by him (Waite 1914, p. 127, Pl. 3), from a litter of 36 taken from a female measuring 1398 mm. Solution of this question is, however, a matter for the future.

On the Magellanic shark named *C. macracanthus* by Regan (1906, p. 436), the dorsal fin spines (first as well as second, Fig. 12 E, F) project farther from the skin than they do in any of the other representatives of the genus discussed so far, though not as much as is suggested by Regan's (1906, p. 437) characterization of them as "strongly projecting." Its two dorsal fins also — especially the first — are larger relatively than in the specimens of **coelolepis* and of **owstoni* that we have seen, more nearly paralleling *plunketi* in this respect.[15] And the distance between the inner ends of its preoral clefts is nearly as long as

[15] We are indebted to Dr. Ethelwyn Trewavas and to Mr. Denys W. Tucker of the British Museum (Natural History) for tracings of the first and second dorsal fins, and to Dr. Ethelwyn Trewavas for the accompanying drawing of a lower tooth (Fig. 12 G), and for other details of the type specimen.

between the inner ends of the nostrils, to judge from Regan's (1906, p. 436) statement "length of anterior labial fold about equal to its distance from the symphysis." The flank denticles are tridentate on the type (and only known) specimen, but the latter is so small (640 mm. long, Regan 1906, p. 437) that this may represent a transitory state; those on mature specimens may be of a different shape, as they are in **C. coelolepis* (p. 87).

In the species of *Centroscymnus* so far mentioned, the gap between the inner ends of the preoral clefts is at least ¾ as long as the distance between the nostrils. In the three named species yet to be considered (**crepidater* and **jonsonii* of the northeastern Atlantic; *rossi* of the Indian Ocean) the clefts are so much longer that the space between their inner ends is only about one-third as long as between the nostrils (Figs. 1D, 12B). Other than this, the most sharply diagnostic features of **crepidater* are that its flank-denticles are tridentate on large specimens (Fig. 12D), as they also are in *C. plunketi* (p. 89), and that its first dorsal fin spine projects from the skin nearly as far as in *C. macracanthus* (cf. Fig. 12A with 12E, F).

The original (and only detailed) account of **C. jonsonii* (Saemundsson 1922, p. 192, Pl. 5) does not include any comparison with **crepidater,* nor does it suggest any definite ground for considering it as distinct from the latter. Comparison of seven specimens (male and female, 587-796 mm. long) from south of Iceland and southwest of the Faroes[16] with the 787 mm. female from Madeira (Fig. 12A), on which Günther (1870, p. 421) based his first-hand account of **crepidater,*[17] has revealed no significant differences, whether in teeth, in the shape of the denticles on large specimens, in bodily proportions (p. 93), or in the shapes, the sizes or the relative locations of fins. Consequently we have no hesitation in classing **jonsonii* as a synonym of **crepidater,* the known range of which extends (on this basis) from Madeira and the coast of Portugal northward to the Faroes and southern Iceland.

[16] Kindly made available to us by the Natural History Museum, Reykjavik, and by the University Zoological Museum, Copenhagen.

[17] We owe to the British Museum the opportunity to examine this specimen. Its identification as **crepidater* has been checked through correspondence with Dr. A. M. Ramalho, who has contributed measurements and photographs of the teeth of the type specimen which he has examined in Lisbon on our behalf.

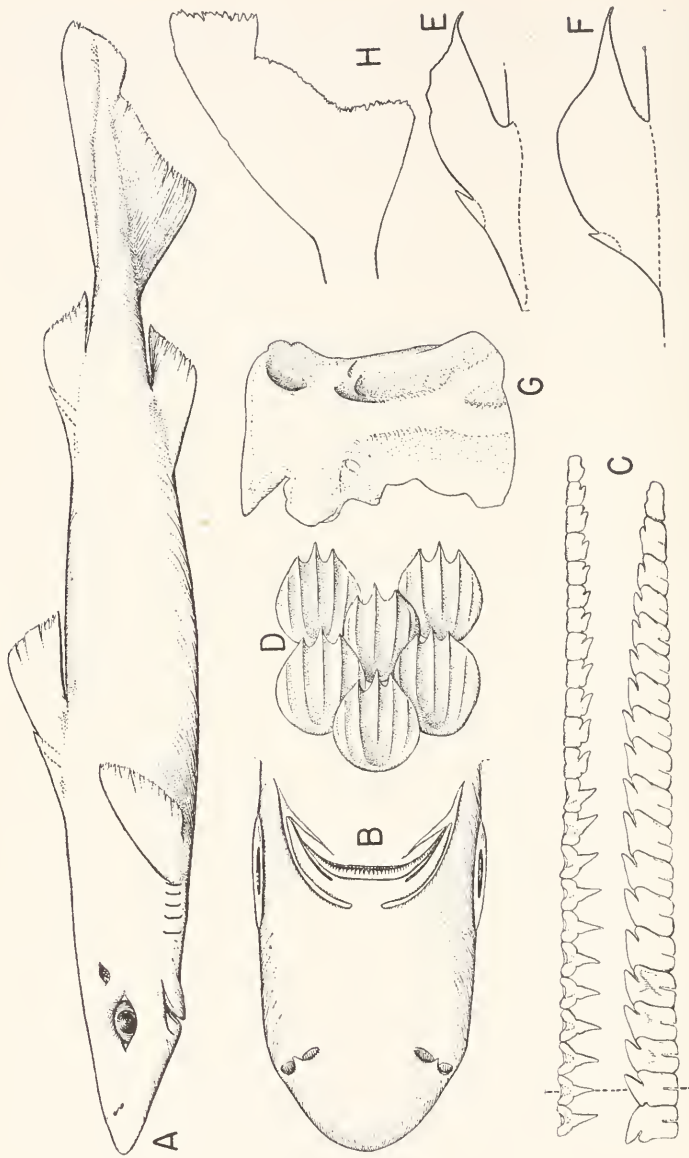

FIGURE 12

Dr. J. A. F. Garrick informs us, also,[18] that the Canterbury Museum contains two specimens of a shark taken on a long line set at 914 meters (500 fathoms) off Keikoura, New Zealand, and two others presumably from New Zealand but without definite locality, that differ from **crepidater* (including **jonsonii*) of the eastern North Atlantic only in such minor particulars that it is doubtful whether specific separation is warranted. And this we can corroborate, for we find no significant differences in bodily proportions, fins, teeth or denticles between one of these New Zealand specimens (kindly sent us by Dr. Garrick) and the Atlantic specimens that we have seen of **crepidater* (pp. 93-94).

Proportional dimensions in per cent of total length of **Centroscymnus crepidater*. A, female, 787 mm., Madeira, from the British Museum (Natural History); B, four females, 746 to 796 mm. long and C, male, 587 mm. long, off Iceland and the Faroes, from the University Zoological Museum, Copenhagen; D, female, 822 mm. long, presumably from New Zealand (see above), Mus. Comp. Zool. No. 39570.

Fig. 12. A, *Centroscymnus crepidater*, female, 787 mm. long, from Madeira, in British Museum. B, lower surface of head of same, to show the great length of the preoral clefts. C, upper and lower teeth of same, x about 2.3. D, denticles of same, from side below first dorsal fin, x about 6.5. E, *Centroscymnus macracanthus*, outline of first dorsal fin of a female, 640 mm. long, type specimen, in British Museum, from Magellanic region. F, outline of second dorsal fin of same; E and F, after tracings of the fins kindly contributed by Mr. Denys W. Tucker. G, third right hand lower tooth of same, x about 7, from drawing kindly contributed by Dr. Ethelwyn Trewavas. H, *Centroscymnus coelolepis*, caudal fin of female, 1035 mm. long, from offing of Delaware Bay, Mus. Comp. Zool. No. 38295.

[18] Information contributed by Dr. Garrick in advance of publication.

	A	B	C	D
Trunk at origin of pectoral: breadth	8.9	8.3-9.3	8.7	9.0
height	7.4	6.7-8.8	8.2	7.1
Snout in front of: eye	8.6	8.2-9.3	8.3	8.9
mouth	11.4	11.4-12.7	11.7	11.8
Eye: horizontal diameter	4.4	4.4-4.6	4.6	4.5
Mouth: breadth	6.1	6.1-7.5	7.5	7.1
Nostrils: distance between inner ends	3.3	3.1-3.6	3.2	3.6
Preoral clefts: distance between inner ends	1.1	1.1-1.3	1.0	0.7
Gill opening lengths: first	1.5	1.3-1.5	1.4	1.3
third	1.5	1.3-1.5	1.4	1.3
fifth	1.5	1.3-1.8	1.6	1.6
First dorsal fin: vertical height	5.2	5.1-5.5	5.4	4.6
length of base from origin of spine	7.5	5.9-6.7	7.0	6.6
Second dorsal fin: vertical height	4.8	4.3-5.9	5.4	5.0
length of base from origin of spine	7.1	6.3-6.8	7.0	7.3
Caudal fin: upper margin	22.2	19.0-20.7	20.8	18.9
lower anterior margin	13.2	10.7-13.5	13.0	13.4
Pectoral fin: width	5.3	5.2-6.8	4.2	5.2
length of anterior margin	13.1	11.8-13.1	11.4	12.4
Distance from snout to: first dorsal	28.9	28.1-30.5	30.7	29.2
second dorsal	60.2	61.0-64.2	60.3	61.7
upper caudal	77.8	79.3-81.5	79.2	81.1
pectoral	24.4	23.7-24.1	24.7	23.3
pelvics	60.6	61.0-65.0	56.3	62.2
Interspace between: origins of first and second dorsal spines	30.9	28.0-31.5	32.0	29.5
second dorsal and caudal	6.1	6.9-8.0	7.0	7.7
pelvics and caudal	8.0	7.4-8.8	10.0	7.9
Distance from origin to origin of:				
pectorals and pelvics	36.1	36.6-40.7	31.7	40.5
pelvics and caudal	15.8	15.2-17.9	17.9	15.7
Teeth, number of series: uppers	43	39-48	51	36+[19]
lowers	36	32 36	32	36+[19]

This adds to the list of cases among sharks and skates where a species, or pair of very closely allied species, is known from temperate latitudes in the two hemispheres, but not from the tropical-subtropical belt that intervenes.

C. rossi from the Indian Ocean, if represented correctly in Alcock's (1899, Pl. 26, Fig. 3) illustrations, differs from **crepidater* in a much longer head, and in detail as to the unpaired fins, especially the caudal which appears to lack the subterminal

[19] Several teeth have been lost at the corners of the mouth.

notch; perhaps also in the shapes of the teeth, though the illustrations of the latter by Alcock appear to be somewhat diagrammatic. The denticles on the sides of the trunk are strongly tridentate on juveniles (represented by the type specimen 254 mm. long), much as they are in **C. coelolepis* (Bigelow and Schroeder 1954, p. 48, Fig. 2B); the shape is not known for adults.

The relationship of *C. fuscus* of southern African waters to other members of its genus remains doubtful, for while it falls with **coelolepis* in length of snout, in the sizes and relative positions of fins, and in the concave crowns of the denticles on the sides of its body when mature (type and only known specimen 1,100 mm. long),[20] the length of its preoral clefts is not known. And the characterization of it in the original description (Gilchrist and von Bonde 1924, p. 2, our only source of information) as with orbits 1.7 times as long as the snout ("orbit .6 in snout") seems an obvious error, for this would credit it with eyes far larger than those of any related shark.

Key to Species of *Centroscymnus*

1. Distance between inner ends of preoral clefts at least 75 per cent as long as distance between nostrils 2
   Distance between inner ends of preoral clefts is not more than about 30 per cent as long as distance between nostrils C
2. Exposed part of first dorsal fin spine, measured along its anterior margin, is very nearly 50 per cent as long as distance from its point of emergence from the skin to rear end of base of the fin (Fig. 12F) ..
   macracanthus Regan 1906.
   Magellanic region. p. 90
   Dorsal fin spines exposed only at their extreme tips, if at all 3
3. Both of the dorsal fin spines are wholly concealed by the skin .....
   cryptacanthus Regan 1906.
   Madeira. p. 88
   The tips of the dorsal fin spines protrude more or less from the skin ..4
4. First dorsal fin, from point of emergence of spine to rear end of base, is about as long as second dorsal fin, similarly measured . **coelolepis*
   Bocage and Capello 1864.
   North Atlantic, east and west. p. 88
   First dorsal fin, from point of emergence of spine to rear end of base, is shorter than second dorsal fin, similarly measured 5

[20] Apparently the type specimen has been lost (Smith 1949, p. 58).

5. Snout in front of mouth is at least as long as from mouth to level of first gill openings ..... **owstoni* Garman 1906. Japan. p. 89

   Snout in front of mouth is noticeably shorter than from mouth to level of first gill openings ....*plunketi* Waite 1910. New Zealand. p. 89; also *waitei* Thompson 1930, New Zealand, perhaps a young stage of *plunketi* (see discussion, p. 90).

6. Head, to level of origin of pectoral fins, is only about 24-25 per cent of total length; caudal fin with distinct subterminal notch ..... **crepidater* Bocage and Capello 1864, including **jonsonii* Saemundsson 1922. Eastern North Atlantic. p. 91; also New Zealand, or represented there by a close ally (see discussion, p. 93).

   Head to level of origin of pectoral fins about 31 per cent of total length, caudal fin without distinct subterminal notch ..... *rossi* Alcock 1898. Indian Ocean. p. 94

   Systematic position in the genus doubtful ..... *fuscus* Gilchrist and von Bonde 1924. Southern Africa, see discussion, p. 95.

Genus SCYMNODON Bocage and Capello 1864

Scymnodon Bocage and Capello 1864, p. 263; 1866, p. 31, type species **S. ringens* Bocage and Capello 1864, p. 263; 1866, p. 32, Pl. 1, fig. 1; Pl. 3, fig. 2A; type locality off Portugal.

Generic Synonyms:

Centrophorus in part, Günther 1870, p. 423, for **Scymnodon ringens* Bocage and Capello 1864.

Zameus Jordan and Fowler 1903, type species *Centrophorus squamulosus* Günther 1877, Japan.

Not *Centrophorus* Müller and Henle 1837, type species **Squalus granulosus* Bloch and Schneider 1801.

Generic characters. As in *Centroscymnus* (p. 85), except with the upper teeth much longer midway along each side of jaw than either toward the center of the mouth or toward its outer corners (Fig. 13C). Lower teeth triangular, highest and symmetrical along median sector of jaw, shorter but only weakly

oblique toward outer corners of mouth; first and second dorsal fin spines scarcely projecting beyond the skin; dermal denticles on sides of trunk scale-like, tridentate, the outer surface with longitudinal ridges alone in some species, including the type but also with cross ridges (Fig. 13, F, G) in one species (*obscurus* Vaillant 1888) that seems referable to *Scymnodon* by its dentition.

Maximum recorded length 1100 mm. for *ringens* (Bocage and Capello 1866, p. 32).

Depth range. One of the four known representatives of this genus has been reported from a depth as great as 1400-1435 meters (one specimen, Vaillant 1888, p. 68); a second, *squamulosus* (Günther 1887, p. 6), from 631 meters. A young specimen, however (the only one known) of a third was found on the beach at North Brighton, New Zealand (Archey 1921, p. 195). No information in this respect is at hand for the type species of the genus, so far known only from Portugal and from the northern coast of Spain (Rey 1928, p. 457).

Remarks. Günther (1870, p. 420) thought that "the passage . . . from reclining to erect teeth in the lower" jaw is too gradual to justify the separation of *Scymnodon* from *Centroscymnus;* or the separation of either of these from *Centrophorus,* for that matter. But the difference in dentition between the species referred here to *Scymnodon* and those referred to *Centroscymnus* (p. 88) is in fact so conspicuous that a glance at the mouth is enough to place a given specimen in the one category or in the other (provided it is properly referable to either), which makes the retention of *Scymnodon* as a separate genus a matter of convenience, even if nothing more.

The contrast is also interesting between the pointed or tridentate denticles, with longitudinal ridges, on the sides of the trunk on mature specimens of *Scymnodon* and the replacement of denticles of this type by evenly rounded ones with concave blades, in some of the species of *Centroscymnus* (p. 86). But this difference can no longer be regarded as alternative between the two genera, for the denticles are tridentate in the adults of two of the species (**crepidater* Bocage and Capello 1864, and *plunketi* Waite 1909), the teeth of which place them in *Centroscymnus* (p. 88). In any case choice of the denticles rather than of the dentition as the primary distinction between *Scym-*

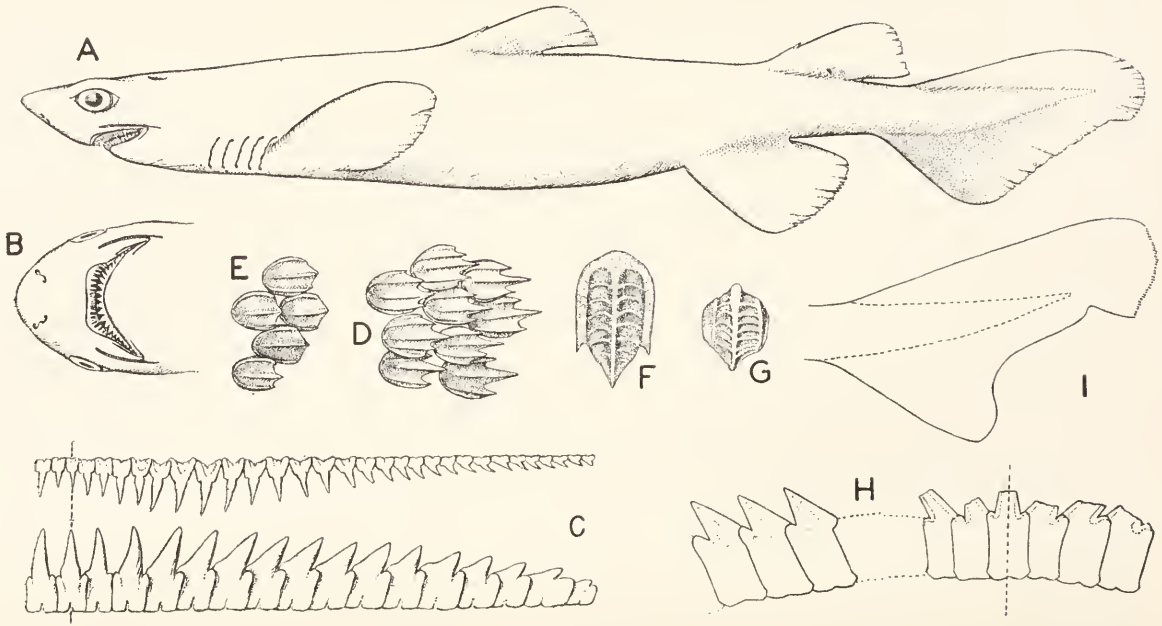

FIGURE 13

nodon and *Centroscymnus,* as by Garman (1913), by Fowler (1941), and by Bigelow and Schroeder (1948) would provide no basis on which to refer a given specimen to the one genus rather than to the other, unless it chanced to be full grown or nearly so. While the only illustration of one of the three known species of *Scymnodon* (*squamulosus* Günther 1877) shows no sign of fin spines, the artist seems to have overlooked them, for Günther (1887, p. 6, Pl. 2, Fig. B) wrote of them as "very small, scarcely projecting beyond the skin."

Species: Named species referable to *Scymnodon* as defined here are: **S. ringens* Bocage and Capello 1864, type species, offing of Portugal; *Centrophorus squamulosus* Günther 1877, Japan; and *Centroscymnus obscurus* Vaillant 1888, off the coast of northwestern Africa,[21] in a haul from 1400-1435 meters. The New Zealand shark, also, that was described by Archey (1921) as *Scymnodon sherwoodi* has been retained in that genus by the several authors (Whitley 1934, 1940; Fowler 1941; Bigelow, Schroeder and Springer 1953; and Richardson and Garrick 1953), who have had occasion to refer to it. But we now learn from Dr. J. A. F. Garrick[22] that the type (and only known) specimen, which he has recently examined, shows no trace of a spine in either of its dorsal fins, and that it is therefore one

Fig. 13. A, *Scymnodon ringens,* female, 893 mm.. long, coast of Portugal, in British Museum. B, ventral view of anterior part of head of same. C, upper and lower teeth of same, left hand side of mouth, x about 1, midpoint of jaws marked by the dotted line. D, dermal denticles of same, from side below first dorsal fin, x about 7. E, dermal denticles of same from side of caudal peduncle x about 7. F, *Scymnodon obscurus,* dermal denticle of type specimen, female, 590 mm. long, off northwest Africa (p. 100), from side below first dorsal fin, x about 18, made available to us through kindness of Dr. P. Budker. G, dermal denticle of same, after Vaillant, 1888, Pl. 2, Fig. 2. H, lower teeth of same, from drawing contributed by Dr. P. Budker, x about 4. I, *Scymnodon squamulosus,* type specimen, female, 658 mm. long, Japan, in British Museum, outline of caudal fin from drawing contributed by Mr. Denys W. Tucker.

[21] The locality as given by Vaillant (1888, p. 68), is "sur les côtes du Soudan," a designation referring to the general region from southern Morocco to Senegal (Folin, 1887, pp. 287-300).

[22] Information contributed by Dr. Garrick in advance of publication.

of the Dalatiinae not of the Squalinae, as the sub-families are defined here (p. 18).

We have pointed out elsewhere (Bigelow and Schroeder 1954, p. 51) that the juvenile shark from the northwestern Atlantic, on which Bigelow, Schroeder and Springer (1953, p. 233) based their new species **Scymnodon melas,* actually represented a juvenile stage in the growth of **Centroscymnus coelolepis* Bocage and Capello 1864.

The dentition of *obscurus* closely resembles that of **ringens,* as Dr. Paul Budker has kindly verified for us from examination of the type specimen of *obscurus* in the Paris Museum. Indeed, Garman (1913, p. 208) has definitely rated *obscurus* as a synonym of **ringens.* But a more abruptly truncate caudal fin, with more definite subterminal notch and smaller pectorals in *obscurus* (as pictured by Vaillant 1888, Pl. 2, Fig. 2) than in **ringens,* and flank denticles with a double series of transverse ridges between the more prominent longitudinal ridges (Fig. 13, F, G; see also Vaillant 1888, Pl. 2, Fig. 2C) argue against this union, hence *obscurus* is retained here as a distinct species. It is interesting, also, that in *obscurus* some of the denticles on the sides of the trunk of a given individual may be tridentate, while others are not (Fig. 13, F, G).

The Japanese *squamulosus* (Günther 1887, p. 5, Pl. 2, Fig. B) agrees with **ringens* in the shape of its denticles. But an examination of the type specimen in the British Museum by Mr. Denys W. Tucker (to whom we are greatly indebted), shows its gill openings as only about 50 per cent as long, relatively, as those of **ringens;* its snout as longer relatively and more pointed (length from tip of snout to mouth about as great as distance between inner ends of preoral clefts); and both its second dorsal, its pectoral and ventral fins, also its caudal (Fig. 13, I), as differing so conspicuously from those of **ringens,* that the two species are clearly distinct. In all these respects, indeed, *squamulosus* so nearly resembles *obscurus* (as pictured by Vaillant 1888, Pl. 2, Fig. 2) that these two species might easily be confused. But the denticles on the sides of the trunk of *squamulosus* (as pictured by Günther 1887, Pl. 2, fig. B) show no trace of the transverse ridges that mark the denticles of *obscurus* (Fig. 13, F, G).

Key to Species of *Scymnodon*

1. Lower outline of caudal fin nearly continuously rounded, with subterminal notch only faintly marked, and without definite lower-anterior lobe (Fig. 13A); pectoral fin, when laid back, reaching very nearly to a perpendicular at base of first dorsal fin spine ..... **ringens* Bocage and Capello 1864, eastern North Atlantic. p. 99

   Lower outline of caudal fin with well-marked subterminal notch and prominent lower anterior lobe (Fig. 13, I); pectoral fin, when laid back, falls short of a perpendicular at base of first dorsal fin spine by a distance at least 50 per cent as long as snout anterior to eyes 2

2. Outer surface of dermal denticles on sides of trunk with weak transverse ridges in addition to the three longitudinal ridges (Fig. 13, F, G). ..... *obscurus* Vaillant 1888, off coast of Northwestern Africa. p. 100

   Outer surface of dermal denticles on sides of trunk without transverse ridges ..... *squamulosus* Günther 1877, Japan. p. 100

Genus DEANIA Jordan and Snyder 1902

Deania Jordan and Snyder 1902, p. 80, type species, **D. eglantina* Jordan and Snyder, Japan.

Generic Synonyms:

Acanthidium in part, Lowe, 1839, p. 92, for **A. calceum* Lowe, Madeira.

Centrophorus in part, Lowe, 1843, p. 93, and subsequent authors, for *C. calceus* Lowe 1843, equals **Acanthidium calceum* Lowe 1839.

Centrophorus in part, Bocage and Capello 1864, 1866, for *C. crepidalbus* Bocage and Capello, evidently equals **Acanthidium calceum* Lowe 1839.

Scymnodon in part, Goode and Bean 1895, by error, their Pl. 4, Fig. 12, labelled "*S. ringens* Bocage and Capello" in the explanation of plates being a copy of the illustration by Bocage and Capello (1866, Pl. 2, Fig. 1) of *Centrophorus crepidalbus* Bocage and Capello 1864, equals *Acanthidium calceum* Lowe 1839.

Nasisqualus Smith and Radcliffe 1912, p. 681, type species **N. profundorum* Smith and Radcliffe, Philippines.

Acanthidium Garman 1913, p. 215; type designated as **A. calceum* Lowe 1839; but incorrectly so, because **A. pusillum* Lowe 1839 (which is a species of *Etmopterus* Rafinesque 1810, see below) had previously been designated as the type of *Acanthidium* by Jordan and Evermann (1896, p. 55).

Daeniops Whitley 1932, p. 36, type species *Acanthidium quadrispinosum* McCulloch 1915, Australia.

Not *Centrophorus* Müller and Henle 1837, type species **Squalus granulosus* Bloch and Schneider 1801.

Not *Acanthidium* Lowe 1839, type species **A. pusillum* Lowe as designated by Jordan and Evermann 1896, p. 55, and by Jordan 1919, p. 195, making *Acanthidium* a synonym of *Etmopterus* Rafinesque 1810 (see above).

Not *Scymnodon* Bocage and Capello 1864, 1866, type species **S. ringens* Bocage and Capello 1864.

Generic characters. Inner corner of pectoral fins rounded in most species, perhaps rectangular in some, but not extended (p. 103); snout in front of mouth longer than from mouth to level of origin of pectoral fins; preoral clefts only very slightly expanded inwardly; dermal denticles on sides of trunk high, pitchfork shaped; teeth smooth-edged in all known species; other characters as in *Centrophorus* (p. 64).

Maximum recorded lengths, 1138 mm. (*quadrispinosa* McCulloch 1915, p. 100); 1070 mm. (*kaikourae* Thompson 1930, as "*calceus*"); and 1060 mm. (*calcea,* Vaillant 1888, p. 71).

Depth range. The depths of capture so far recorded for *Deania* (mostly, at least, in the trawl, hence subject to the uncertainty emphasized on p. 5) are: 605-1431 meters for *calcea* (Roule 1919, p. 119); 715-1785 meters for **profundorum* (Smith and Radcliffe 1912, p. 683); 190-366 meters for **eglantina* (Smith 1949, p. 58); and 238-823 meters for *quadrispinosa* (McCulloch 1915, p. 100; Whitley 1940, p. 147). While definite information as to depth is wanting for *kaikourae,* it was reported from "deep water" (Thompson 1930, p. 276, as "*calceus*"). And the Japanese records for **aciculata* (Garman) 1906, **rostrata* Garman 1906, and *hystricosa* (Garman) 1906 which we here refer to **eglantina* (p. 104) were from the deep line-fishery in Sagami Bay. Evidently *Deania* can fairly be termed a deep-water genus.

Remarks. The chief respects in which the various species that have been grouped together as *Deania* (or as one or other of its synonyms) differ from *Centrophorus* are: a much longer snout, and pitchfork-shaped denticles on the sides of the body. Most of the species of *Deania* are set further apart from *Centrophorus* by the rounded shape of the inner corner of their pectoral fins. But the two genera intergrade in this respect, the inner corner of the pectorals being quadrate, both in one member of *Centrophorus* (*foliaceus* Günther 1877), as noted above (p. 66), and

also in one member of *Deania*, if Gilchrist's (1922, Pl. 7, Fig. 2) illustration of his *D. natalense* represents the latter correctly.[23]

Deania differs from *Centroscymnus* and from *Scymnodon* in a much longer snout; in a longer exposed portion of the second dorsal fin spine; and in broader upper teeth. It differs further from *Scymnodon* in that the teeth in the central part of its upper jaw are nearly or quite as long as those midway out along either side. It had appeared also until recently that its high, pitchfork-shaped denticles were equally diagnostic of *Deania* as contrasted with *Centrophorus* and with the *Centroscymnus-Scymnodon* group. But Garrick (1955, p. 234, Fig. 2) has found that the denticles on the sides of the trunk of young specimens of *Centroscymnus waitei* (Thompson) 1930 of New Zealand (p. 90) approach the pitchfork-like shape that was formerly thought to be diagnostic of the denticles of *Deania*.

The cusps of the upper teeth of *Deania* are sharp-tipped, rather narrowly triangular, with concave margins, on broad bases;[24] erect along the central part of the jaw, but increasingly oblique toward the outer corners of the mouth.

The lower teeth are very strongly oblique all along either side, and the median tooth is not symmetrical in the female of any species for which the condition in this respect is known. In **calcea* (Lowe) 1839 (the oldest species), the lowers are of the same shape in the males as in the females, as illustrated by a male of 848 mm. and a female of 1037 mm. that we have seen from southwest of the Faroes.[25] Similarly, the lowers are described and pictured as strongly oblique in the male in **profundorum* (Smith and Radcliffe 1912, p. 681, Pl. 53), which we can verify from our examination of the type specimen. But the lowers are described by McCulloch (1915, p. 101) as much less strongly oblique in the males of *quadrispinosa*, from Australia, than in the females, which is also the case in the Japanese species-complex that we unite here (p. 104) under the name **eglantina* Jordan and Snyder 1902. Thus the lowers (including the median tooth) of the female pictured by Garman

[23] The pectoral fins are not mentioned in Gilchrist's (1922, p. 49) description of his *natalense*.

[24] Our re-examination of the type specimen of **Deania eglantina* (type of the genus) has shown that Jordan and Snyder's (1902, p. 81) description of the teeth as with "small basal cusp" is not correct.

[25] We are indebted to Dr. J. R. Pfaff, of the University Zoological Museum, Copenhagen, for the opportunity of seeing these specimens.

(1913, Pl. 11, Fig. 7) as *Acanthidium hystricosum*[26] are shown as strongly oblique, whereas those of the adult male figured by him (Garman 1913, Pl. 12, Fig. 2) as **Acanthidium aciculatum* (which we have examined) are erect in the front of the mouth, with the median tooth symmetrical. And the reserve rows of lower teeth of an immature male, 682 mm. long, in the Museum of Comparative Zoology, are similarly nearly erect along the center of the jaws (the functional row is badly worn). The situation in this respect is not known for *natalense* or for *kaikourae*.

It is a matter of common knowledge that sexual dimorphism of this sort is common among batoid elasmobranchs, but it seems not to have been reported previously among sharks.

Species: Named species referable to *Deania:* are **Acanthidium calceum* Lowe, 1839, eastern Atlantic; **Deania eglantina* Jordan and Snyder 1902, type species, Japan; **Acanthidium aciculatum* Garman 1906, *A. hystricosum* Garman 1906, and **A. rostratum* Garman 1906, all from Japan; **Nasisqualus profundorum* Smith and Radcliffe 1912, Philippines; *Acanthidium quadrispinosum* McCulloch 1915, Australia; *Acanthidium natalense* Gilchrist 1922, Natal, southeastern Africa; and *Centrophorus kaikourae* Whitley 1934, New Zealand, which was originally reported and pictured by Thompson (1930, p. 275, Pl. 42 as *Centrophorus calceus* Lowe).

Our re-examination of the type specimens of **eglantina* (a female of 300 mm.), **aciculata* (a male of 890 mm.) and **rostrata* (a female of 873 mm.) has revealed no differences between them in proportional dimensions (see below) greater than may reasonably be credited to the difference between them in stage of growth, or to the variability that has already been reported by Regan (1908, p. 52) for the allied **calcea* of the Atlantic. Cases in point are the somewhat longer head and caudal fin, but shorter interdorsal space of the **eglantina*. And while the type specimen of the fourth member of this group (*hystricosa*) is no longer to be found, Garman's (1913, Pl. 11, Figs. 5-8) beautiful illustrations of it, by the well-known zoological artist E. N. Fischer, do not suggest anything to set it apart either. Hence, all deanias yet reported from Japan are referred here to the one species **eglantina* Jordan and Snyder 1902.

[26] This specimen is no longer to be found.

Proportional dimensions in per cent of total length. A. **Deania eglantina,* female, 300 mm., type, U.S.N.M. No. 49524; B. **D. rostrata,* female, 873 mm., type, M.C.Z. No. 1047; C. **D. aciculata,* male 890 mm., type, M.C.Z. No. 1128; all from Japan.

	A	B	C
Trunk at origin of pectoral: breadth	9.3	7.5	6.7
height	7.7	8.0	6.7
Snout in front of: outer nostrils	5.3	5.3	4.0
mouth opening	15.3	13.7	12.1
Eye: horizontal diameter	5.3	3.6	4.7
Mouth: breadth	7.7	5.6	6.4
Nostrils: distance between inner ends	4.5	3.4	3.4
Preoral clefts: distance between inner ends	4.8	3.4	3.7
Gill opening lengths: first	2.0	—	1.7
third	2.0	2.5	1.7
fifth	2.0	2.1	1.8
First dorsal fin: vertical height	3.8	3.5	2.9
length of base from spine origin	9.5	9.7	11.8
Second dorsal fin: vertical height	4.7	5.5	4.8
length of base from spine origin	9.2	10.0	10.0
Caudal fin: upper margin	20.0	16.0	16.8
lower anterior margin	11.6	10.8	9.8
Pectoral fin: width	6.2	6.1	6.1
length of anterior margin	9.3	9.0	8.9
Distance from snout to: 1st dorsal spine	42.3	39.9	40.2
2nd dorsal spine	68.2	70.5	70.5
upper caudal	80.0	84.0	83.2
pectoral	28.7	24.0	23.2
pelvics	61.6	64.7	62.6
Interspace between: origins of first and second dorsal spines, at base	24.6	30.5	30.7
second dorsal and caudal	3.8	3.2	3.4
pelvics and caudal	8.9	10.3	10.1
Distance from origin to origin of:			
pectorals and pelvics	33.3	40.8	39.3
pelvics and caudal	13.3	13.4	14.4
Teeth, number of series: uppers	28	34	29
lowers	13-1-14	?	29

The Japanese **eglantina* (including Garman's supposedly distinct species, as just noted), is so closely allied to **Deania calcea* of the eastern Atlantic that Regan (1908, p. 51) has already relegated it unequivocally to the synonymy of **calcea,* and

**aciculata* doubtfully so. But it seems to us wiser to retain **eglantina* as a separate species, at least until a large number of specimens of the Japanese and North Atlantic populations have been studied, for while the Japanese specimens listed above agree very closely indeed with the two **calcea* we have seen, in fin characters and in bodily proportions in general, the lower teeth are as oblique in the males of **calcea* as in the females, but are more erect in mature males than in females in **eglantina,* as noted above (p. 103). Though this last difference would not be an aid to identification unless the species in hand chanced to be well-grown males, it deserves taxonomic recognition of some sort. And the question as to whether the North Atlantic and North Pacific populations of this general type have diverged significantly since they became isolated geographically, one from the other, is one too interesting to be answered offhand.

The **calcea-*eglantina* group of the Northern Hemisphere has close counterparts, in the Southern Hemisphere, in *quadrispinosa* of Australia; also in a shark reported and pictured from southern African waters by Smith (1949, p. 58, Fig. 49) as **eglantina,* which certainly resembles the type specimen of **eglantina* very closely. But the eventual decision as to the identity of either or both of these with **eglantina* of Japan must await the comparison of specimens from the different ocean areas.

In the **calcea-*eglantina-quadrispinosa* group (however many species this may eventually prove to represent), the pectoral fins, when laid back, fall considerably short of a vertical at the point of emergence from the skin of the first dorsal fin spine. But the pectorals of **profundorum* from the Philippines are pictured as reaching rearward to abreast of the first dorsal spine (Smith and Radcliffe, 1912, Pl. 53), and our own examination of the type specimen has shown this to be correct. As this is a rather conspicuous difference, **profundorum* may be accepted as a good species.

The original illustration of *natalense* (Gilchrist 1922, Pl. 7, Fig. 2) of southern African waters, shows the pectorals not only as reaching rearward beyond the first dorsal spine, but also with the inner corner quadrate, instead of rounded as they are in other known representatives of the genus *Deania.* But Smith's (1949, p. 58) allocation of it (with *quadrispinosa*) to the synonymy of **eglantina* — perhaps from examination of the type

which Barnard (1925, p. 51) has reported as being in the collection of the Government Marine Survey of South Africa — suggests that the artist's representation of *natalense* may not have been correct. Hence its status remains in doubt, pending further information.

Finally, *kaikourae* (falling with the **calcea-*eglantina* group in length of pectoral fin) differs from all other known members of *Deania* in a first dorsal fin base about 1.6 times as long as the second (each measured from the point of emergence of the respective fin spine from the skin), contrasted with 0.9-1.2 times for the **calcea-*eglantina-quadrispinosa* group, for **profundorum*, and for *natalense*. Thompson (1930, p. 276) indeed, has already called attention to this feature in his original account of *kaikourae* (as "*Centrophorus calceus*").

To sum up, the nine representatives of the genus *Deania* that have been named from various seas may represent as few as four species, **calcea* in the North Atlantic, **eglantina* in the North and South Pacific and southern Indian Ocean, *kaikourae* from New Zealand, and **profundorum* in Philippine waters. Or they may represent as many as six, if *quadrispinosa* from Australia, and the South African form reported by Gilchrist 1922 as *natalense*, but by Smith (1949) as **eglantina*, should finally prove to be separable, not only from **eglantina* of the North Pacific, but one from the other as well.

Key to Species of *Deania*

1. Pectorals, when laid back, falling considerably short of a perpendicular at point of emergence of first dorsal fin spine from the skin 2
   Pectorals, when laid back, reach at least as far as a perpendicular at point of emergence of first dorsal fin spine 4
2. First dorsal fin, from point of emergence of spine to rear end of base is 1.5-1.6 times as long as second dorsal, similarly measured .....
   kaikourae Whitley 1934, Australia, p. 107
   First dorsal fin, from point of emergence of fin spine to rear end of base of fin, is only 0.9-1.2 times as long as second dorsal fin, similarly measured 3
3. Lower teeth as strongly oblique in males as in females .....
   **calcea* Lowe 1939.
   Northeastern Atlantic, including Mediterranean, p. 105
   Lower teeth more erect in males than in females .....**eglantina*

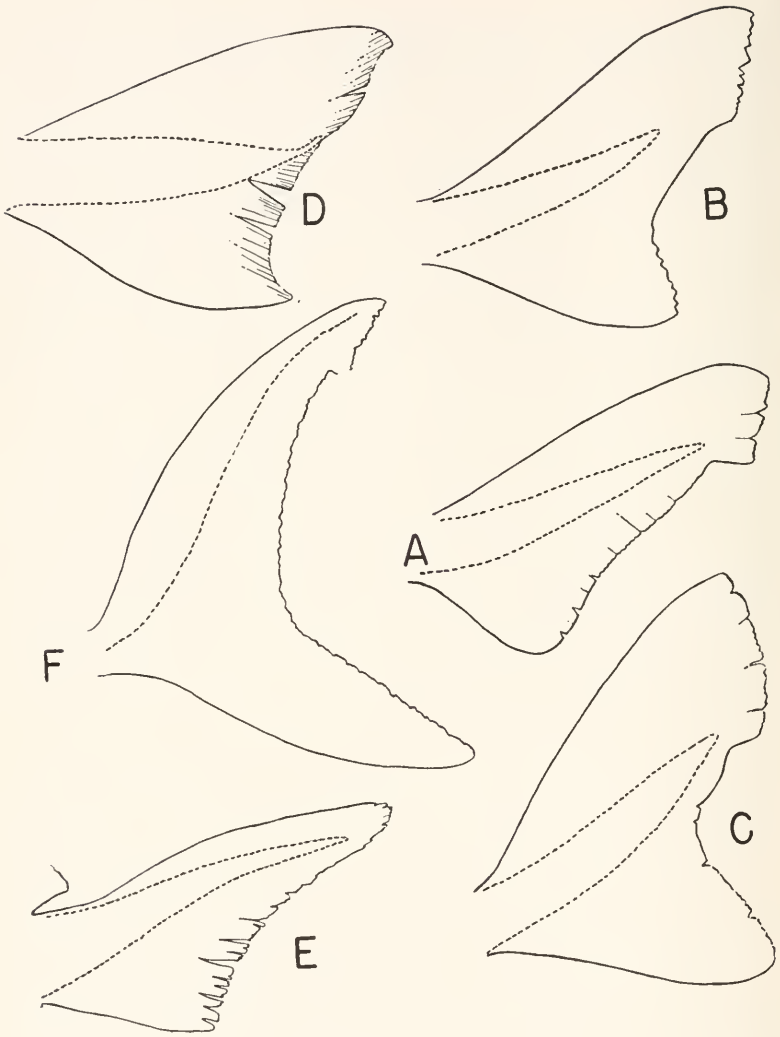

FIGURE 14

Jordan and Snyder 1902 (incl. **aciculata* Garman 1906, **rostrata* Garman 1906, and *hystricosa* Garman 1906), Japan, and reported from southern Africa (p. 106); also *quadrispinosa* Gilchrist 1922, Australia. p. 106

4. Inner corner of pectoral fins rounded; first dorsal fin only about 70 per cent as high vertically as second dorsal fin ..... **profundorum* Smith and Radcliffe 1912, Philippines. p. 106

Inner corner of pectoral fins quadrate; first dorsal fin about as high vertically as second dorsal fin .....*natalense* Gilchrist 1922. Off Natal coast, southern Africa (but see discussion). p. 107

Subfamily DALATIINAE

Subfamily characters. Squalidae lacking a second dorsal fin spine (lacking a first spine also in most cases); preoral clefts lacking in most but present in one of the known genera (*Scymnodalatias*, p. 124); dermal denticles either truncate with hollow crown, or with a single cusp or spine; teeth with only one cusp, the uppers narrow, awl shaped or lancet shaped; the lowers much broader, with quadrate base, each overlapping the next outward; caudal axis raised in some but not in others; the caudal fin varying widely in shape accordingly (Fig. 14), its tip more or less evidently truncate; sides of body, anterior to cloaca, without longitudinal ridges.

Fig. 14. Outlines of caudal fins of representative genera, adjusted to equal lengths along upper margin, to show relative breadth of fin above axis and below; also degree to which caudal axis is raised. A, *Dalatias licha*, male, 1114 mm. long, Japan, Mus. Comp. Zool. No. 1116. B, *Somniosus microcephalus*, male, 1334 mm. long, Massachusetts Bay, Mus. Comp. Zool. No. 39609. C, *Isistius brasiliensis*, male, 383 mm. long, western North Atlantic north of the Bahamas, Mus. Comp. Zool. No. 36039. D, *Squaliolus laticaudus*, same specimen as in Fig. 16A. E, *Echinorhinus brucus*, male, 1650 mm. long, Mauritanian coast, northwest Africa, Mus. Comp. Zool. No. 39633. F, *Lamna ditropis*, type specimen, male, 2085 mm. long, off La Jolla, California, Mus. Comp. Zool. No. 36471, the vertebral axis indicated by the broken line.

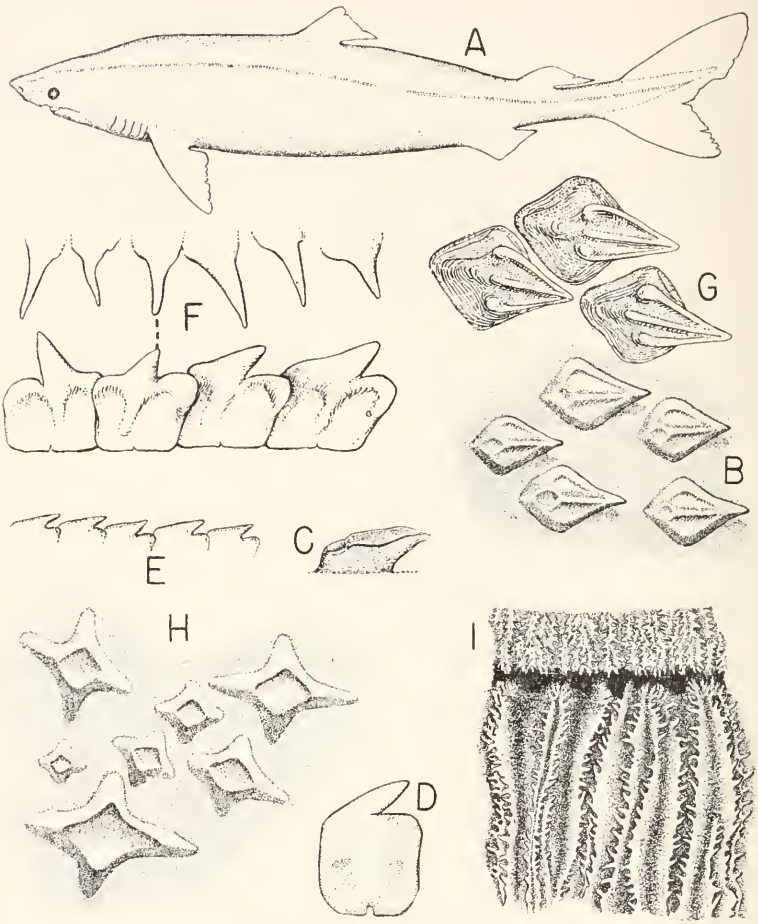

FIGURE 15

Genera. The shark species referable to this admittedly "artificial" group have been distributed among the following named genera: (1) *Dalatias* Rafinesque 1810, type species *D. sparophagus* Rafinesque, equals **Squalus licha* Bonnaterre 1788; (2) *Somniosus* Lesueur 1818, type species *S. brevipinna* Lesueur, equals **Squalus microcephalus* Bloch and Schneider 1801; (3) *Euprotomicrus* Gill 1864, type species *Scymnus* (*Laemargus*) *labordii* Müller and Henle 1841, equals **Scymnus bispinatus* Quoy and Gaimard 1824; (4) *Isistius* Gill 1864, type species **Scymnus brasiliensis* Quoy and Gaimard 1824; (5) *Heteroscymnus* Tanaka 1912, type species **H. longus* Tanaka; (6) *Squaliolus* Smith and Radcliffe 1912, type species **S. longicaudus* Smith and Radcliffe; (7) *Heteroscymnoides* Fowler 1934, type species **H. marleyi* Fowler; (8) *Pseudoscymnus* Herre 1935, type species *P. boshuensis* Herre; and (9) *Scymnodalatias* Garrick 1956, type species *Scymnodon sherwoodi* Archey 1921. There seems nothing, however, to set *Pseudoscymnus* apart from *Dalatias* (Bigelow and Schroeder 1948, pp. 501, 502). And Hubbs and McHugh's (1951, p. 164, Footnote) suggestion that *Heteroscymnus* should be reduced "perhaps to the synonymy of *Somniosus,*" is supported by our examination of the teeth (Pl. 3) and denticles (Fig. 15B) of the one known species, **H. longus* Tanaka 1912, from Japan. For further discussion of it see page 121.

Fig. 15. A, *Somniosus longus,* type specimen, female, 1360 mm. long, Japan, after Tanaka, the shapes of the fins somewhat emended to accord with a Japanese male, 1010 mm. long, Mus. Comp. Zool. No. 39650, kindly contributed by Dr. Tokiharu Abe. B, dermal denticles of latter, from side below first dorsal fin, x about 25. C, side view of same. D, *Somniosus rostratus,* lower tooth of Mediterranean female, 820 mm. long, after Canestrini, 1864, Pl. 2, Fig. 4. E, lower teeth near center of jaw, of Portuguese shark described by Capello 1870 under the name "*rostratus*", traced from a photograph contributed by Dr. A. M. Ramalho. F, *Heteroscymnoides marleyi,* type specimen (see Fig. 16E), upper and lower teeth at center of mouth, x about 12. G, dermal denticles of same, from side below first dorsal fin, x 36. H, *Squaliolus laticaudus,* same specimen as in Figure 16A, denticles on side below first dorsal fin, x about 45. I, *Dalatias licha,* same specimen as in Figure 14A, a sector of the exposed part of upper and lower lips, x about 4.

In short, the dozen or so known species of Dalatiinae that appear to deserve separate recognition seem referable to 6 or 7 genera as defined by the positions and relative sizes of the first and second dorsal fins, presence or absence of a spine on the first dorsal fin, nature of the teeth, shape of the dermal denticles on the sides of the body, and degree to which the portion of the caudal fin above the axis is developed relative to the portion below the axis. This last matter is one of especial interest, as already stressed by Hubbs and McHugh (1951, p. 164) in their key to genera, for in the genera in which the fin is the most widely expanded above the axis (Fig. 14), the latter is raised only very slightly above the main axis of the shark's body (if at all). In other words, one of the evolutionary trends of the group has been a tendency for the tail to lose the heterocercal nature so characteristic for it among sharks in general. Caudal fins even more lunate in form (Fig. 14F) are, it is true, well known characteristics of the isurid, basking, and whale sharks. But in all of these the caudal axis is steeply raised; they are, in a word, as truly heterocercal as any other shark, more noticeably so, indeed, than many, such as the erectolobids, scyliorhinids and some of the triakids.

Key to Genera of Dalatiinae

1. Lips with a complex series of fringed cross folds (Fig. 15, I); margins of lower teeth regularly serrate ..... *Dalatias* Rafinesque 1810. p. 113
   Lips smooth, or nearly so; margins of lower teeth smooth, or only faintly and partially serrate at most 2
2. First dorsal fin with a spine, the tip either exposed or buried in the skin ..... *Squaliolus* Smith and Radcliffe 1912. p. 128
   First dorsal fin with no trace of a spine 3
3. Preoral clefts present; upper margin of caudal fin about twice as long as lower anterior margin ..... *Scymnodalatias* Garrick 1956. p. 124
   No preoral clefts; upper margin of caudal fin not more than 1.5-1.7 times as long as lower anterior margin, and relatively shorter than this in most 4
4. Rear end of base of first dorsal fin is over or posterior to origin of pelvic fins; interspace between first and second dorsal fins is shorter than between second dorsal fin and origin of upper margin of caudal; lower teeth erect, symmetrical ..... *Isistius* Gill 1864. p. 123

Rear end of base of first dorsal fin is clearly anterior to origin of pelvics; interspace between first and second dorsal fins is at least as long as between second dorsal fin and origin of upper side of caudal; lower teeth asymmetrical, the cusp more or less strongly oblique, outward 5

5. Origin of first dorsal fin is about over axil of pectorals ..... *Heteroscymnoides* Fowler 1934. p. 182

Origin of first dorsal fin is posterior to tips of pectorals when these are laid back 6

6. Base of first dorsal fin about as long as base of second dorsal; eye only about 20-25 per cent as long as snout in front of mouth ..... *Somniosus* Lesueur 1818. p. 115

Base of first dorsal fin only about 25-33 per cent as long as base of second dorsal; eye more than 50 per cent as long as snout in front of mouth ..... *Euprotomicrus* Gill 1864. p. 126

Genus DALATIAS Rafinesque 1810

Dalatias Rafinesque 1810,[a] p. 10; type species *D. sparophagus* Rafinesque, Mediterranean, equals **Squalus licha* Bonnaterre 1788, designated by Jordan, Tanaka and Snyder 1913. For generic synonyms and references, see Bigelow and Schroeder 1948, p. 501.

Generic characters. Dalatiinae with blade-like lower teeth, the cusp erect, triangular, with serrate edges, the base quadrate with a conspicuous notch on the outer edge marking the transition from cusp to base. Snout in front of mouth much shorter than from mouth to level of first gill openings; longest gill openings about 8-11 per cent as long as head to origin of pectorals (specimens measured); lips only moderately expanded at corners of mouth, and without special cartilages, but conspicuously thick and fleshy inward along each jaw and close-set with a complex series of cross folds with finely fringed edges (Fig. 15, I); furrow from corner of mouth reaching rearward about 30 per cent of distance towards first gill openings; no preoral clefts, but with voluminous subdermal pouches extending forward from the oral pockets (Fig. 1E); caudal fin of the shape shown in Fig. 14A, its axis rather steeply raised; origin of first dorsal fin much nearer to rear edge of pectorals when these are laid back than to origin of pelvics; second dorsal fin about 1.3 times as long as first dorsal at base; no spine in either of the dorsal fins. Denticles on sides of body thick, quadrate, outer surface with three weak ridges united rearward in a point that varies

in length and in acuteness from denticle to denticle; denticles on lower side of snout overlapping, ovate, without marginal teeth (Bigelow and Schroeder 1948, Fig. 96, D, E).

Greatest recorded length, 1820 mm. (Duméril 1865, p. 452).

Depth range. Definite depths of capture that we have found recorded for *Dalatias* in one part of the oceans or another have ranged from about 90 meters down to 600 meters. Probably it is more numerous in the shoaler part of its vertical range, else fishermen would hardly be as familiar with it as they have long been in the eastern side of the North Atlantic, from northwestern Africa and the Canaries to the Irish slope; also in the Mediterranean.

Remarks. The serrate lower teeth of *Dalatias,* and the shape of its caudal fin, with its conspicuously fleshy and complexly sculptured lips, set it so sharply apart that there is no danger of confusing it with any other genus of Dalatiinae.

Species. It is probable that all the reports for *Dalatias* that have appeared in scientific literature during the past century and a half have been based on the single species **D. licha* (Bonnaterre) 1788, type of the genus, which was originally described from "Cap Breton" on the coast of Brittany, by Broussonet (1780, p. 677), as "La Liche." In the eastern side of the Atlantic, **licha* is now known to be generally distributed from tropical West Africa (Rio de Oro), Morocco, the western Mediterranean, the Canaries, and Madeira to the Irish Atlantic slope and to the fishing grounds west of Ireland. Contrasting with this widespread occurrence, and with its local abundance in the Mediterranean and near Ireland, there have been only two published records of its capture in the western Atlantic, the one for a female of about 5 feet (about 1550 mm.), taken on Georges Bank, August 19, 1937 (Nichols and Firth 1939, p. 85; Bigelow and Schroeder 1948, p. 502); the other for an 845 mm. female from the northern part of the Gulf of Mexico (Bigelow, Schroeder and Springer 1955, p. 10). But the recent capture by "Oregon" of a female only about 380 mm. long (U. S. Nat. Mus. No. 157844) in the northern side of the Gulf, suggests that the latter may harbor a resident population.

**D. licha* has also been reported under its own name by Smith (1949, p. 56) from southern Africa, whence it had previously been recorded as a separate species (*D. brevipinnis* Smith

1936, p. 1); from New Zealand; from Australia; also from Japan both as *licha* and as *americanus* Gmelin 1789 (an obvious synonym for *licha*). Identification as *licha* in the case of the Japanese form is corroborated by our own comparison of a Japanese specimen with the specimens we have seen from Georges Bank and from the Gulf of Mexico. (For the list of New Zealand, Australian and Japanese references for **licha,* see Bigelow and Schroeder 1948, p. 508.) Nor do we find anything in Herre's (1935, p. 124) account of the Japanese shark for which he proposed the new generic and specific names *Pseudoscymnus bohuensis* to suggest that it differs in any way from **D. licha.* And this applies equally to McCulloch's (1914, p. 81, Pl. 14) excellent account and illustration of the Australian shark that he described as "*licha*" but which Whitley (1931, p. 310; 1940, p. 151) rechristened *phillippsi,* although without including any supporting evidence to justify the new specific name.

With the known range of **D. licha* so extensive, it seems astonishing that the genus has not been reported as yet from the eastern side of the Pacific, south or north, or from the southern Atlantic, though it is known from Algoa Bay, southeastern Africa.

Genus SOMNIOSUS Lesueur 1818

Somniosus Lesueur 1818, p. 222; type species *S. brevipinna* Lesueur, Massachusetts, equals **Squalus microcephalus* Bloch and Schneider 1801.

For generic synonyms, see the list given by Bigelow and Schroeder 1948, p. 514, with the addition of *Heteroscymnus* Tanaka 1912, type species *H. longus* Tanaka, Japan (see p. 121).

Generic characters. Dalatiinae, without fin spines; teeth smooth edged, the lowers with the cusp directed so strongly outward in some species that the inner edges function as a nearly unbroken cutting edge parallel with the jaw, but more nearly erect in others (Pl. 3); snout in front of mouth at least not longer than from mouth to level of first gill openings; longest gill openings about 9-11 per cent as long as head to origin of pectorals on specimens measured; lips not conspicuously thick, their surface smooth; furrows from corners of mouth reaching rearward only about 35-40 per cent of the distance toward first gill openings; no preoral clefts but with voluminous preoral pouches extend-

ing forward from oral pockets; caudal fin with upper division widely expanded, as well as the lower (Fig. 14B); upper margin about 1.5 times as long as lower anterior margin. Caudal axis moderately raised. Origin of first dorsal fin nearer to rear edge of pectorals (when these are laid back) than to origin of pelvics; second dorsal fin not larger than the first dorsal; interspace between first and second dorsal fins 1.7-3 times as long as between second dorsal and caudal; denticles on sides of body conical to thorn-like, curved rearward, differing widely in size from species to species, and in degree of elevation from the skin.

Size. The different species of *Somniosus* differ widely in size. Thus *rostratus* is not known to grow longer than about one meter. But *microcephalus* averages 8-14 feet (2.4-4.3 meters) at maturity, with specimens of 16-18 feet (4.9-5.5 meters) taken occasionally, and one of 21 feet (6.4 meters) definitely recorded (see Bigelow and Schroeder 1948, p. 519 for further information).

Depth range. The best known member of the genus (**microcephalus*, p. 117) has long been known to occupy a wide depth range, coming right up to the ice in the northern part of its range (Greenland, Labrador) in winter, but in summer most often caught at 180-550 meters, with one recorded from 1207 meters. (For further details see Bigelow and Schroeder 1948, p. 521.) And the depth range is, presumably, about the same for its representative in the North Pacific (*pacificus*, p. 121), though precise information is lacking. The only definite depth record we find for *S. rostratus* of the eastern Atlantic, said by Tortonese (1937-1938, p. 75) to occur off Portugal in shoal water as well as deep, is about 1000 meters, near Madeira, by line fishermen's report (Maul, 1955, p. 7). And the only information at hand in this respect for **S. longus* of Japan (p. 121) is that the specimens so far seen were the product of the deep hook and line fishery in Sagami Bay, Tanaka 1912a, p. 104).

Remarks. The combination of a very short snout with a caudal of the shape shown in Figure 14B, a first dorsal fin originating near the mid-length of the trunk, a second dorsal not larger than the first, and thorn-like denticles, with lower teeth more or less strongly oblique, and razor sharp, makes the recognition of

a *Somniosus* easy, even as one is dumped on deck from the trawl.

The caudal fin in *Somniosus* has a distinct subterminal notch in the specimens we have seen from the Gulf of Maine, from Iceland, and from Japan; indeed it has been so pictured for *rostratus* by Burkhardt (1900, p. 564, Fig. 3) and by Helbing (1904, Pl. 9, fig. 1); for **microcephalus* by Helbing (1904, Pl. 9, fig. 2, as "*borealis*"); by Garman (1913, Pl. 15, fig. 4), and by Bigelow and Schroeder (1948, Fig. 100); by Tanaka (1912a, Pl. 26) for **longus*. Since it is similarly notched on the type specimen of **S. pacificus* Bigelow and Schroeder 1944, from Japan (pictured by Garman 1913, Pl. 15, fig. 1, under the name "*brevipinna*"), we suspect that Tanaka's (1911, Pl. 11, fig. 32) earlier illustration of it for that species (under the name *microcephalus* Bloch and Schneider 1801) as without a notch, represents the result either of wear, or of mutilation.

More significant from the taxonomic standpoint is the wide expansion of the fin above the caudal axis, and its sublunate shape (Fig. 14B).

One species (*rostratus* of the Mediterranean and adjacent Atlantic) is brilliantly luminescent. For a first hand account of its luminescence, and of its light-producing organs, see Burkhardt 1900, p. 560.

Species. The following named species (listed here in chronological order) fall in *Somniosus*:

**Squalus microcephalus* Bloch and Schneider 1801, boreal-subarctic latitudes in the eastern Atlantic; **Somniosus brevipinna* Lesueur 1818, corresponding zone in the western North Atlantic; *Scymnus rostratus* Risso 1826, Mediterranean and Madeira; **Heteroscymnus longus* Tanaka 1912, Japan; *Somniosus antarcticus* Whitley 1939, Macquarie Island, Subantarctica, south of Australia; **Somniosus pacificus* Bigelow and Schroeder 1944, Japan, probably also northeastern Asiatic coast, and American coast from Bering Strait southward to Puget Sound, occasionally to southern California.

Our own comparison of a 1334 mm. male, taken off the coast of Massachusetts, with a 1564 mm. male from Iceland corroborates the view, now generally held, that the Greenland sharks of the subarctic on the two sides of the Atlantic (including the White Sea) and of the neighboring parts of the Arctic Ocean

belong to a single species. How closely the population of **S. microcephalus* in the two sides of the North Atlantic agree in proportional dimensions appears from the following tabulation: A, for a male, 1334 mm. long taken near Boston Lightship in 32 fathoms (Mus. Comp. Zool. No. 39609) and B, for a second male, 1564 mm. long, taken northwest of Iceland, Lat. 66°48′N., Long. 25°10′W., in 180 fathoms, October 1952 (Mus. Comp. Zool. No. 37826).

Proportional dimensions in per cent of total length

	A	B
Snout length in front of: outer nostrils	3.1	2.4
eye	7.3	6.4
mouth	10.3	9.3
Eye: horizontal diameter	2.2	2.4
Mouth: breadth	6.7	7.2
Nostrils: distance between inner ends	3.9	3.4
Gill opening lengths: first	1.8	2.0
second	2.0	2.2
third	2.0	2.2
fourth	2.0	2.2
fifth	1.8	2.0
First dorsal fin: vertical height	3.4	3.5
length of base	7.6	8.4
Second dorsal fin: vertical height	2.9	2.6
length of base	6.6	5.8
Caudal fin: upper margin	20.5	20.6
lower anterior margin	14.9	15.0
Pectoral fin: outer margin	12.1	13.2
inner margin	6.0	5.6
greatest width	6.5	6.2
Distance from snout to: first dorsal	41.2	38.0
second dorsal	65.3	64.9
upper caudal	79.5	79.4
pectorals	24.6	24.6
pelvics	59.7	59.3
Interspace between: first and second dorsals	16.5	18.3
second dorsal and upper caudal	7.7	8.7
pelvics and lower caudal	12.1	11.6
Distance between origins of: pectorals and pelvics	35.2	34.8
pelvics and subcaudal	17.1	17.0
Teeth:	48/48	45/51

This joint species was originally described by Gunnerus in 1766 under the name *Squalus carcharias,* but by the rules of nomenclature, it must be called **microcephalus* Bloch and Schneider 1801, "the name *Squalus carcharias* having been used previously by Linnaeus 1758, for a very different shark" (Bigelow and Schroeder 1948, p. 515). The known range of **microcephalus* extends from the White Sea, Bear Island, Spitzbergen and east and west Greenland, southward to the North Sea (to the mouth of the Seine as a straggler) in the east, to the Gulf of Maine in the west.

A second North Atlantic species, *rostratus* Risso 1826, resembles **microcephalus* so closely in general appearance that as recently as 1928 Rey (1928, p. 480), following Garman (1913, p. 241), classed it as identical with the former, while — to further confuse the issue — recent illustrations of *rostratus* by Burkhardt (1900, p. 564, fig. 3) and by Maul (1955, Pl. 3, fig. 17) differ as to the length of the upper side of the caudal peduncle relative to the length of the base of the second dorsal fin. Both, however, like Canestrini (1864, Pl. 2, fig. 2) and Helbing (1904, Pl. 9, fig. A) show the distance from the rear tip of the second dorsal to the origin of the upper side of the caudal as less than 70 per cent as long as the base of the second dorsal (about as long as the base of the second dorsal in **microcephalus*). A more important difference is that the lower teeth are pictured as with the cusp more nearly erect in *rostratus* (Fig. 15D, see also Maul 1955, Pl. 3, fig. 19) than they are in **microcephalus* (Pl. 3), and its denticles as rising less steeply from the skin (cf. Maul 1955, Pl. 3, fig. 20, with Bigelow and Schroeder 1948, fig. 101B).

Rostratus is also much the smaller member of the pair, the greatest length we find definitely recorded for it being only 1000 mm. (Helbing 1904, p. 347); whereas adults of **microcephalus* average 8-14 feet (2.4-4.3 meters) long, with a few growing considerably larger still (p. 116). A further difference already remarked upon by Burkhardt (1900, pp. 561-562, 565) is that while the luminescent organs of *rostratus* (p. 117) are surrounded and thus rendered conspicuous by denticles that differ in blunter cusps and more definitely stellate bases from those elsewhere on the sides, this is not the case in **microcephalus,* as we can verify from our own examination of a well

preserved male 1334 mm. long, taken off Massachusetts. For that matter, we have not been able to detect anything suggestive of luminescent organs on it, or on a 1564 mm. male from Iceland (p. 118).

Helbing (1904), also, in his extensive treatise on the anatomy and systematic relationships of *Somniosus* (as *"Laemargus"*), has pointed out several skeletal differences between *rostratus* and **microcephalus* (as *"borealis"*). Finally, *rostratus* is ovoviviparous (see Helbing 1904, p. 358, for illustration of its embryos at successive stages in growth), as are all the other genera of Squaloidea for which the mode of development is known, whereas it is still an open question whether **microcephalus* is ovoviviparous or oviparous (for a summary of available evidence, see Bigelow and Schroeder 1948, p. 520).

For a more detailed discussion of the differences in proportional dimensions between *rostratus* and **microcephalus*, see Tortonese 1937-1938, p. 74.

It has recently been suggested by Maul (1955, p. 9) that the Portuguese shark described and pictured under the name *rostratus* by Capello (1870, p. 148, Pl. 9, fig. 2) actually represents a third Atlantic species of *Somniosus* (as yet unnamed), for it is shown and described as differing from *rostratus* in a longer snout and head, and as with the position of the second dorsal fin different in relation to the pelvics, to which we may add a longer caudal pedunele. This appears from the following comparative dimensions of (A) *rostratus* according to Maul (1955, measurements, p. 9, and fig. 17), and of (B) the Portuguese specimen reported under that name, from Capello's measurements, and illustration, also measurements, contributed by Dr. A. M. Ramalho, who kindly re-examined the specimen now in the Bocage Museum in Lisbon.

	A	B
Length of head, to pectorals, in per cent of total length	20	28-29
Snout to mouth, in per cent of length of head	25	35
Distance from rear end of base of 2nd dorsal to upper origin of caudal, in per cent of total length	7	11

Also, the origin of the second dorsal, pictured as opposite the rear end of the bases of the pelvics by Maul, for his Madeira specimen, is about 10 mm. posterior to the pelvics on the Capello specimen, as we are informed by Dr. Ramalho, while excellent photographs of its mouth, supplied by him (Fig. 15E) show its lower teeth as somewhat more strongly oblique than they are pictured for the typical *rostratus* (Fig. 15D after Canestrini, 1864, Pl. 2, fig. 4; see also Maul 1955, fig. 19), i.e., resembling, rather, those of *microcephalus*. Thus, present indications are that the Capello specimen may well represent an undescribed species more nearly related to **microccphalus* than to *rostratus*. But it seems to us wiser to leave the matter open than to burden shark literature with a new name that might soon be relegated to oblivion.

The early reports of *Somniosus* from the North Pacific, west and east, were either as "*microcephalus*" or as "*brevipinna,*" on the assumption that the Pacific representative of the genus was identical with the Atlantic **microcephalus*. And the Japanese specimen, on which we based our new species *pacificus* (described and pictured by Garman 1913, p. 240, Pl. 15, figs. 1-3, as "*brevipinna*"), agrees with **microcephalus* (p. 117) in lacking any evident dermal structures to which a luminescent nature might be ascribed, and in the shape of its lower teeth. But its first dorsal stands considerably farther rearward than on the Atlantic specimens that we have seen of **microcephalus*, or than is pictured for *rostratus;* the distance from the tip of its second dorsal to the origin of the upper side of its caudal is shorter relative to the size of the second dorsal; the upper posterior and lower anterior margins of its caudal are more convex; and its upper teeth are broader. It was because of these differences that we proposed the new species **pacificus* for it (Bigelow and Schroeder 1944, p. 35). And it seems reasonably certain (though not yet proven) that the various reports of *Somniosus* from northeastern Asia, Alaska, and thence southward along the Pacific Coast of America to California all were based on this same species.

Japanese waters also harbor a second *Somniosus* (Fig. 15A, B, C, Pl. 3), the **Heteroscymnus longus* of Tanaka 1912a (p. 102, Pl. 26, figs. 102-107), more nearly resembling *rostratus* than either **microcephalus* or **pacificus* in the shape of its lower

teeth, in the minuteness of its denticles, and in the length of the base of its first dorsal fin relative to the length of the head. So closely, indeed, does Tanaka's account of its type specimen, corroborated by our examination of a female of about 1010 mm. (in rather poor condition), received from Dr. Tokiharu Abe, agree with the published accounts of *rostratus* (we have not seen that species) that it is doubtful whether the Japanese population differs consistently enough in any respect from the Atlantic population to deserve a separate specific name — final decision is a matter for the future.

Somniosus has not been reported from tropical-equatorial waters. But the *microcephalus-pacificus* division of the genus is represented in subantarctic latitudes by *S. antarcticus* Whitley 1939, a name proposed for an "8 foot, 2 inch" (2491 mm.) specimen that was found stranded on the beach at Macquarie Island in latitude about 54°49′S., south of Australia (Waite 1916, p. 51, fig. 10).

The position of its first dorsal fin, as pictured by Waite, and the shape of its caudal suggests a closer resemblance to **microcephalus* of the northern Atlantic than to **pacificus*. But final decision as to its specific relationship must await a more detailed study of the Southern Hemisphere population.

Key to Species of *Somniosus* in the Northern Hemisphere

1. Lower teeth only moderately oblique (Fig. 15D); adults with evident luminescent organs, at least in best known species (see p. 117) ..... *rostratus* Risso 1826. Mediterranean and Madeira; p. 119; also *longus* Tanaka 1912a, Japan, perhaps not distinguishable from *rostratus*, see discussion, p. 121.

   Lower teeth so strongly oblique that the inner margins are almost parallel with the trend of the jaw, forming a nearly uninterrupted cutting edge (Pl. 3); no evident luminescent organs 2

2. Head to pectorals 28-30 per cent of total length; lower teeth as in Fig. 15E .....*rostratus* Capello 1870 (*not* of Risso 1826), off Portugal; see discussion, p. 120.

   Head to pectorals only about 24-26 per cent of total length 3

3. Origin of first dorsal much nearer to tip of snout than to tip of caudal; interspace between first and second dorsals as long as from snout to 1st-2nd gill openings or longer ....
**microcephalus* Bloch and Schneider 1801. Both sides of northern North Atlantic. p. 117.

Origin of first dorsal almost as near to tip of caudal as to tip of snout; interspace between first and second dorsals only about 66 per cent as long as from tip of snout to second gill openings .....
**pacificus* Bigelow and Schroeder 1944. Type locality Japan, probably also northeastern Asia and Pacific Coast of North America, from Bering Sea south to Puget Sound, occasionally to southern California. p. 121.

Genus ISISTIUS Gill 1864

Isistius Gill 1864, p. 264; type species **Scymnus brasiliensis* Quoy and Gaimard 1824, off Brazil.

Generic characters. Dalatiinae without dorsal fin spines; lower teeth symmetrically triangular and smooth-edged, or only faintly and irregularly serrate; snout in front of mouth shorter than from mouth to first gill openings; lip fold at corners of mouth smooth but greatly expanded (Fig. 1F; Bigelow and Schroeder 1948, fig. 98B), and supported by special cartilages that are easily felt; groove at corners of mouth extending rearward for about half (44-57 per cent) of the distance toward first gill openings (Bigelow and Schroeder 1948, fig. 98B); no preoral clefts, but with voluminous subdermal pouches extending forward from oral pockets (Fig. 1F); gill openings minute, only about 4.3-4.4 per cent as long as head to origin of pectorals on western North Atlantic and Japanese specimens measured; rear end of base of first dorsal fin about abreast of origin of pelvics; second dorsal only very slightly longer at base than first dorsal (1.2 times on specimens measured); interspace between first and second dorsal fins only about 50 per cent as long as between pelvics and lower origin of caudal; caudal fin sublunate, with well-marked subterminal notch, nearly or quite as broad above caudal axis as below, its upper margin about 1.5 times as long as lower anterior margin; the caudal axis raised only very

slightly. Denticles on sides of body truncate, with concave crown.

Maximum recorded length close to 500 mm. (Bigelow and Schroeder 1948, p. 512).

Range. Tropical and subtropical belts of Atlantic, Pacific and Indian Oceans.

Remarks. It has long been common knowledge that the sole known representative of *Isistius* (**brasiliensis* Quoy and Gaimard 1824) is brilliantly luminescent, the entire lower surface of its body (except for the dark collar) shining with a vivid greenish light that presumably is produced by black dots with which the lower surface is strewn densely; the sides, the dorsal and caudal fins, and the basal parts of the pectorals more sparsely so (see Bennett 1840, p. 225, for an eye-witness account of the luminescence; Burkhardt 1900, pp. 555, 556, 565, fig. 5 for the distribution of luminescent dots).

Species. The various reports that have come to hand for *Isistius* from one part of the ocean or another seem all to have been based on the one species that was described first by Quoy and Gaimard (1824, p. 198) from Brazilian waters as **Scymnus brasiliensis*. *Brasiliensis* has subsequently been taken in the Gulf of Guinea, off Sierra Leone and Cape Verde, and north of the Bahamas in the Atlantic; near the Galapagos and the Hawaiian Islands, in Japanese waters, near Fiji, west of Christmas Island, north of New Guinea, near Lord Howe Island off New South Wales, between Java and western Australia and near Mauritius in the Pacific and Indian Oceans. Recent records for the mid-Pacific are of three specimens, taken at the surface in the equatorial belt southward from the Hawaiian group (Lat. 2°04′S, Long. 168°57′W; Lat. 4°47′N, Long. 161°04′W; and Lat. 2°09′N, Long. 158°14′W) where the water is 1000-3000 fathoms (about 1830-5485 meters) deep (King and Ikehara 1956, pp. 18-19). (For a description and list of references, see Bigelow and Schroeder 1948, pp. 509-514, figs. 98-99.)

Genus SCYMNODALATIAS Garrick 1956

Scymnodalatias Garrick 1956, p. 564; type and only known species, *Scymnodon sherwoodi* Archey 1921, p. 195, Pl. 39, New Zealand.

Generic characters. Dalatiinae without dorsal fin spines but

with distinct preoral clefts (see discussion, p. 12); teeth smooth-edged, the uppers "needle-like, with asymmetrically twisted cusps" (Garrick 1956, p. 564), the lowers with triangular cusp much more nearly erect than in *Somniosus;* snout in front of mouth only about as long as from mouth to first gill openings; head to pectorals between 20 and 25 per cent of total length; longest gill openings pictured as about 9 per cent as long as head to pectorals; lips at corners of mouth not conspicuously expanded; furrow from corners of mouth reaching rearward only about 17-20 per cent of distance toward first gill openings; pre-oral clefts, described by Garrick (1956, p. 568) as "upper labial furrows," short, but clearly shown on Garrick's (1956, Pl. 1, figs. A, C) illustrations of type specimen; whether or not expanded inwardly is not known. Caudal fin with distinct subterminal notch; upper margin about twice as long as lower-anterior margin; caudal axis moderately raised; origin of first dorsal fin far in advance of pelvics; second dorsal fin a little larger than first dorsal; interspace between first and second dorsal fins about twice as long as between second dorsal and caudal; denticles on sides below first dorsal fin scale-like, overlapping, the free margins strongly tridentate, with median point considerably the longest, the outer surface with three ridges corresponding to the marginal points.

Size. The state of development of the claspers of a male *sherwoodi,* 803 mm. long (only specimen yet seen) makes it likely that this shark matures sexually when it is 900-1000 mm. long.

Range. So far known only from New Zealand.

Remarks. Archey's (1921, p. 195) original account of *sherwoodi* credits it with dorsal fin spines in the form of "scarcely discernible rudiments imbedded in the skin." Garrick (1956, p. 556), however, on examining the type specimen was unable to find any indication whatever of a spine in either dorsal fin, even on dissection, nor any indication that spines might have been removed. Seemingly what Archey interpreted as spines actually were the "most anterior of the radial cartilages supporting the dorsal fins" (Garrick 1956, p. 556). It is for this reason that we follow Garrick in placing *Scymnodalatias* among the Dalatiinae, rather than among the Squalinae, where Archey (1921) originally located it. Actually it bridges the gap

between the two subfamilies, having a well marked preoral cleft reaching forward from each corner of the mouth (for discussion, see p. 12), and in having upper teeth longer in the middle third of each side of the jaw than either toward the center of the jaw or toward its outer corner, as is true of *Scymnodon* (p. 96).

Scymnodalatias resembles the Japanese **Somniosus longus* (Tanaka 1912a, p. 102) in its bodily proportions in general, as well as in the sizes, shapes and relative positions of the dorsal, pelvic and pectoral fins, and in the shape of its lower teeth. But it differs sharply from all members of the genus *Somniosus* in the shape of its caudal fin (see key, p. 112), and especially in having well marked preoral clefts (see above under Generic Characters). Other differences, seemingly generic, to which Dr. Garrick has called our attention in a recent letter are that the second dorsal fin is larger than the first in *Scymnodalatias*, that the first dorsal stands farther rearward, and that its lower teeth are more erect.

Species. Only one species referable to *Scymnodalatias* has yet been reported, namely the *Scymnodon sherwoodi* of Archey 1921, so far known from a single specimen found on the beach near Canterbury, New Zealand, in 1920. For a detailed and well illustrated account of it, with discussion of its systematic relationships, see Garrick 1956.

Genus EUPROTOMICRUS Gill 1864

Euprotomicrus Gill 1864, p. 264, footnote 4, type species *Scymnus* (*Laemargus*) *labordii* Müller and Henle 1841, p. 94, Islands of Mauritius and Bourbon, Indian Ocean; equals **Scymnus bispinatus* Quoy and Gaimard 1824, p. 197, Pl. 44, figs. 1, 2.[27]

Generic characters. Dalatiinae without dorsal fin spines; the snout blunt, its length in front of mouth about as great as from mouth to level of third gill openings; caudal pedunele without precaudal pits. Head to pectorals between 20 and 25 per cent of total length; lips at corners of mouth thick, fleshy, whether or not with supporting cartilages is not known; no preoral clefts, but with a voluminous pouch extending forward from

[27] In replacing Quoy and Gaimard's (1824) name **bispinatus* with *labordii*, Müller and Henle formalized Quoy and Gaimard's use of "Leiche laborde" as the French vernacular name for this shark, proposed in memory of M. Theodore Laborde.

each oral pocket; groove from corner of mouth reaching rearward for 50-66 per cent of the distance toward first gill openings; gill openings minute (Fig. 16F). First dorsal fin considerably posterior to mid-length of trunk, but its base well in advance of origin of pelvics; second dorsal about 2.5 times as long, at base, as first dorsal; interspace between first and second dorsals a little longer than between second dorsal and caudal; caudal fin without subterminal notch, its upper margin about 1.2 times as long as lower-anterior margin; caudal axis moderately raised and continuing to extreme rear margin of the fin; the fin wider below the axis than above; dermal denticles described as low, quadrate, with concave crowns and of two sizes (Hubbs and McHugh 1951, p. 167), the smaller much the more numerous, the larger with stellate bases, and with additional pits surrounding the axial concavity.[28] Teeth smooth edged; the uppers slender, symmetrical, slightly recurved; the lowers with cusp directed obliquely outward, the successive inner edges at an angle of about 45° with the jaw.

Luminescence. The single known species of *Euprotomicrus* is one of the few sharks that are known to be luminescent, glowing, as described by Dickens (1956), with a greenish light that is given off from its lower surface by "many thousands of small light organs," according to Marshall (1956, p. 73).

Size. Lengths of 233 mm. reported by Hubbs and McHugh (1951, p. 170) and of "8-9 inches" by Günther (1870, p. 428) for the only known species of the genus probably approximate the maximum to which it ordinarily grows, for Duméril (1865, p. 457) described the claspers of a male of 205-210 mm. as having a strong spine on the outerside, i.e., as close to maturity. Similarly, the gravid female, 234 mm. long,[29] recently reported by Dickens (1956) and by Marshall (1956) gave premature birth to six young when brought on board ship. Thus *Euprotomicrus* falls in the same size-group with *Squaliolus* (p. 129) and with the smaller of the species of *Etmopterus* (p. 48).

Species. All the various reports for *Euprotomicrus* (see Garman 1913, p. 235 for synonyms under *bispinatus* Quoy and Gai-

[28] We have detected the smaller denticles alone on the specimen we have seen, and only a few of these, here and there. Seemingly its skin has been largely denuded of its armature.

[29] Information contributed by Mr. N. B. Marshall.

mard 1824 and *E. hyalinus* Eigenmann 1891) seem certainly to have referred to the type species *bispinatus* Quoy and Gaimard 1824, of which we have been fortunate enough to study a female, 161 mm. long, from the North Pacific, west of Johnston Island. For a description of it, with measurements, see King and Ikehara 1956, p. 17. For a description of a somewhat larger female (233 mm. long) taken in 1948 some 500 miles off California, with excellent illustrations, and with discussion of the relationships of the genus, see Hubbs and McHugh 1951. The most recent report is that of a gravid female 234 mm. long, taken from the SS "Kent" in the southern Indian Ocean west of Australia, Lat. 23°10′S., Long. 101°58′E. (Dickens 1956; Marshall 1956).

E. bispinatus is known from the Indian Ocean, near Mauritius and Bourbon as well as west of Australia (see above), from New Zealand waters, from the northern Pacific localities mentioned above, and from between Honolulu and San Francisco (Eigenmann 1891, p. 35, as *E. hyalinus*). Our earlier reference of the genus to the Philippines (Bigelow and Schroeder 1948, p. 500) was based on the misconception that the generic name *Squaliolus* Smith and Radcliffe 1912 is an equivalent.

Evidently this is a pelagic species; the specimen we have seen (see above), the one described by Hubbs and McHugh and the one reported by Capt. Dickens (1956) having all been picked up at the surface at night, where the water is more than 2000 fathoms (about 3660 meters) deep.

Genus SQUALIOLUS Smith and Radcliffe 1912

Squaliolus Smith and Radcliffe, 1912, p. 683. Type species **S. laticaudus* Smith and Radcliffe 1912, p. 685, Pl. 50, Philippines.

Generic characters. Dalatiinae with a short spine in the first dorsal fin, either exposed at the tip (Fig. 16A, D) or wholly enclosed in the skin, but without a spine in the second dorsal fin; snout in front of mouth nearly or quite as long as from mouth to origin of pectorals; head, to pectorals, about 33 per cent of total length; caudal peduncle without precaudal pits; lips at corners of mouth thick and fleshy, as in *Euprotomicrus* (p. 126); no preoral clefts, but with a voluminous pouch extending forward from each oral pocket (Fig. 16C); furrows from corners

of mouth reaching rearward 50-70 per cent of the distance toward first gill openings (Fig. 16A, B). Base of first dorsal spine considerably posterior to a perpendicular at axil of pectorals; second dorsal fin at least twice as long at base as first dorsal, its rear tip reaching to a point about midway between rear end of base of second dorsal and origin of upper side of caudal. Caudal fin sublunate, with bluntly pointed tips and without subterminal notch; upper margin only slightly longer than lower anterior margin; the maximum width of the fin nearly as great above the axis as below (Fig. 16A); caudal axis not raised, except that the extreme tip curves upward at the margin of the fin (Fig. 16A). Teeth smooth edged, uppers slender, symmetrical, somewhat recurved, lowers with cusps directed obliquely outward, the inner edges weakly concave in outline, making an angle of about 33° with the jaw (Fig. 16C); the general contour of the tooth deeply notched on the outer side marking the transition from cusp to base. Dermal denticles rather closely spaced and so prominent that the skin has a pebbled look (Pl. 4), truncate, with concave crowns (Fig. 15H), on four-radiate bases, and varying in size from denticle to denticle.

Size. The type species, *laticaudus*, matures when only about 150 mm. long, to judge from the stage in development of the claspers of the type specimen (Smith and Radcliffe 1912). Thus *Squaliolus* includes the smallest shark for which the size at maturity is known, though it is closely rivalled by *Euprotomicrus* (p. 127), by the smaller of the species of *Etmopterus* (p. 48); also by the smallest of the members of the family Scyliorhinidae among the galeoid sharks. *Sarmenti,* the second known species of *Squaliolus*, grows somewhat larger, the two specimens yet seen having measured 224 mm. and 226 mm. in length (both were females).

Depth range. The two specimens of the type species (*laticaudus*) that have yet been seen were taken in Philippine waters in a beam trawl dragging at about 310 meters (170 fathoms, Smith and Radcliffe 1912, p. 685); they may, of course, have been picked up by the trawl either on its way down or on its way up again (p. 5). The case of the second known species is puzzling, for while the original specimen was caught near Madeira on a long line, presumably fishing at least as deep as

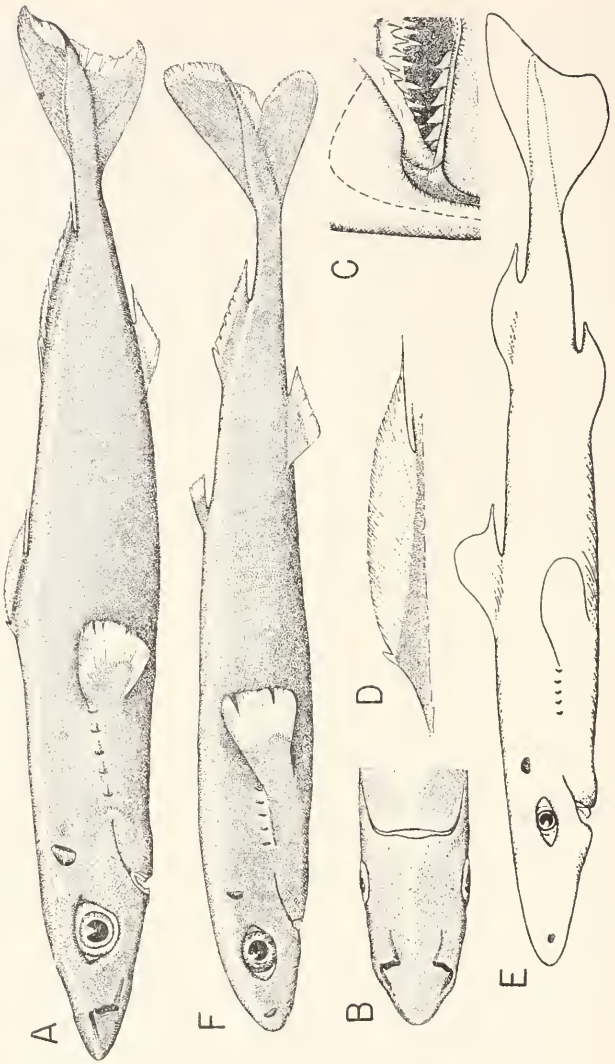

FIGURE 16

900 meters or so (Noronha 1926), the second known specimen was caught in very shoal water, near Arcachon, France, among eel grass (Zostera). (For details see Sigalas 1939-40, p. 70.)

Remarks. In our earlier synopsis of the dalatiine sharks (Bigelow and Schroeder 1948, p. 500, footnote 2) we classed *Squaliolus* as a synonym of *Euprotomicrus,* as had Garman (1913, p. 234) and Fowler (1941, p. 264). Recent examination, however, of the type specimen of *laticaudus* (in the U. S. National Museum), and of the female pictured on Figure 16A has convinced us that *Squaliolus* is separable generically from *Euprotomicrus* from which it is set apart not only by the presence of a spine in the first dorsal fin (it differs in this from all other Dalatiinae for that matter), but also by the position, much farther forward, of its first dorsal fin, by its much longer and more pointed snout, and by its conspicuously longer head.

In the type species each nostril is prolonged at the outer end by a conspicuous groove directed forward, and at the inner end by a similar groove directed rearward (Fig. 16B). But we hesitate to include this feature among the generic characters, because the condition in this respect is not known for the second known representative of the genus (*S. sarmenti,* see below).

Species. Two species referable to *Squaliolus* are known, **S. laticaudus* Smith and Radcliffe 1912, (from the Philippines), type of the genus, and *S. sarmenti* Noronha 1926, which was originally described from Madeira, and which has recently been reported from Arcachon, France, by Belloc (1937) and by Sigalas (1939-40). The chief difference between these two is that while the tip of the first dorsal spine is exposed in **laticaudus* (Fig. 16A, D), it is described by Noronha as entirely enclosed in the skin in *sarmenti.* Other differences mentioned by Noronha

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Fig. 16. A, *Squaliolus laticaudus,* female, 143 mm. long, Philippines, U. S. Nat. Mus., No. 70259. B, ventral view of anterior part of head of same. C, right hand corner of mouth of same, the preoral pouch indicated by the broken curve, x about 4. D, first dorsal fin of same, to show spine, x about 3. E, *Heteroscymnoides marleyi,* after Fowler, slightly emended from comparison with the type specimen, a female, 126 mm. long, from the Durban Coast, southern Africa (see p. 133). F, *Euprotomicrus bispinatus,* female, 161 mm. long, from central Pacific west of Johnson I., U. S. Nat. Mus. No. 164176.

are that the first dorsal fin stands a little farther forward in *sarmenti,* in which the distance from snout to first dorsal origin is about 42 per cent as long as the trunk (about 48 per cent in **laticaudus*), and that the pectorals, when laid back, reach only about as far as the concealed first dorsal spine in *sarmenti,* but overlap the base of the fin in **laticaudus.* It may also prove that *S. sarmenti* lacks the grooves extending from the inner and outer ends of the nostrils that characterize **S. laticaudus,* for they are not indicated on the illustrations of *sarmenti* (Noronha 1926, Pl. 35). But the latter are not clear in this respect.

Genus HETEROSCYMNOIDES Fowler 1934

Heteroscymnoides Fowler 1934, p. 239, type species **H. marleyi* Fowler 1934, p. 240, Durban coast, southeastern Africa.

Generic characters. Dalatiinae without fin spines; snout in front of mouth about as long as from mouth to third gill openings; head (to pectorals) more than ⅓ of trunk (to origin of caudal); gill openings minute, not more than 3-4 per cent as long as head to origin of pectorals; lip at corners of mouth neither conspicuously thick and fleshy nor expanded; furrow at corners of mouth reaching rearward about 40 per cent of the distance toward first gill openings; no preoral clefts; whether or not with preoral pouches is not known; origin of first dorsal fin close behind a perpendicular at origin of pectorals; second dorsal fin about 1.2 times as long (at base) as first dorsal, its origin over bases of pelvics; distance from rear base of second dorsal to origin of upper side of caudal fin about 50 per cent as long as interspace between first and second dorsals; caudal (in excellent condition on the one known specimen) without subterminal notch, about 1.7 times as wide below caudal axis as above; upper margin about 1.3 times as long as lower anterior margin; caudal axis not appreciably raised. Dermal denticles on sides of body (Fig. 15G) triangular spur-like, with three prominent ridges, raised only slightly, on quadrate bases, and so closely spaced that the skin is almost wholly concealed. Upper teeth erect, lowers directed somewhat obliquely outward (Fowler 1941, p. 273).

The size at maturity is not known, the only specimen yet seen being a newly born female, 126 mm. long, with healed umbilical

scar. Presumably this was from shoal water, but the depth of capture is not known.

Remarks. The features that set *Heteroscymnoides* the most obviously apart from related genera are its long snout and head, minute gill openings, shape of caudal fin, and location of the first dorsal fin.

Species. One species only (the type) is known, **H. marleyi* Fowler 1934. For a detailed account, with illustration showing its general appearance, see Fowler's (1934, p. 239; 1941, p. 273) original description of the only specimen that has yet been seen. Having had an opportunity to examine the latter through the kindness of Dr. James Böhlke of the Academy of Natural Sciences, Philadelphia, we include the following table of its proportional dimensions as per cent of total length, with number of teeth.

Snout, length in front of: eye	11.9
mouth	17.1
Eye: horizontal diameter	4.8
Mouth: breadth	8.0
Nostrils: distance between inner ends	4.0
Gill openings: length of longest	1.0
First dorsal fin: vertical height	3.2
length of base	6.4
Second dorsal fin: vertical height	2.8
length of base	8.2
Caudal fin: upper margin	18.3
lower anterior margin	13.9
Pectoral fin: outer margin	10.7
Distance from snout to: first dorsal	34.1
second dorsal	65.8
upper caudal	81.7
pectorals	30.1
pelvics	57.5
Interspace between: first and second dorsals	22.2
second dorsal and caudal	10.0
Distance from origin to origin of: pectorals and pelvics	27.4
pelvics and caudal	21.4
Teeth:	6-1-6
	11-1-11

Subfamily ECHINORHININAE

Squalidae without fin spines; the teeth with several cusps, the median cusp much the largest; upper teeth similar to lowers; caudal axis raised, the fin wider below the axis than above, its tip pointed, without subterminal notch; short preoral clefts, but not expanded inwardly, nor is the pocket at each corner of the mouth extended rearward, furrow-like, as it is in all other known representatives of the family Squalidae; dermal denticles either simple, with central cusp, or compound, with two or more cusps, and varying correspondingly in size on any given individual; lateral line, along sides of body roughened with series of minute thornlets (see *Remarks*, below). Recorded up to 8-9 feet long.

Echinorhinus Blainville 1816 is the only known genus.

Genus ECHINORHINUS Blainville 1816

Echinorhinus Blainville 1816, p. 121; type species *E. spinosus*, no author quoted but doubtless the **Squalus brucus* of Bonnaterre 1788, p. 11, intended.

For generic synonyms, see Bigelow and Schroeder 1948, p. 526.

Generic characters. Those of the subfamily.

Depth range. "In all warm seas from 10-100 fathoms" (18-183 meters), Smith 1949, p. 56.

Remarks. The combination of characters given above under the subfamily, especially the buckler-like denticles, often with 2 or more cusps, and the peculiar armature of the lateral line, would place *Echinorhinus* at a glance, should one come to hand in any part of the world where it is not well known.

Accounts of the lateral line in *Echinorhinus* have been conflicting. Rey (1928, p. 488) who had seen only a dried skin, described it as in the form of a deep furrow enclosed between two close-set rows of slender tentacular structures or dermal papillae, though with the reservation that he could not form an exact idea of it. This is in line with McCoy's (1887, Pl. 144, fig. 1G, reproduced by Whitley 1940, fig. 169) illustration of it as flanked by two sparse rows of flexible papillae. And it was from these sources that our earlier account of it (Bigelow and Schroeder 1948, p. 527) was drawn. McCoy (1887, p. 165), however, described it for his Australian specimen as "roughened

with rows of minute, slender hooked spines" as far forward as the third gill openings. And it is similarly armed with minute, curved, thorn-like spines on an excellent specimen from the Mauritanian Coast that we have received through the kindness of Dr. Ramalho, the only suggestion of papillae or the like being that the course of the channel is marked by numerous shreds of skin and flesh, seemingly the result of wear. In its present state the canal is open along most of its length on both sides of the body. But as seen in cross-section its lower lip overlaps the upper. And since it is bridged over here and there for short stretches by the tissue-paper-thin skin, we assume that normally the canal is closed, at least as far rearward as the pelvic fins, if not farther still. A touch is enough to show that the spinelets are denticular structures, not fleshy. And they are in plain view (under a lens) wherever the canal is open. But we have not been able to determine (because of the condition of the specimen) whether they are exposed at the tips along the short stretches where the canal is roofed over, or whether they are entirely enclosed, as is suggested both by surface views and by cross sections of the canal.

Species. The following named species fall in *Echinorhinus:* **Squalus brucus* (Bonnaterre) 1788 (also reported repeatedly as *spinosus* Blainville 1825), the type of the genus, well known in the eastern North Atlantic; *Echinorhinus obesus* Smith 1849, Pl 1, South Africa; *E. cookei* Pietschmann 1928, p. 297; 1930, p. 3, Fig. 1, Hawaiian Islands; and *E.* (*Rubusqualus*) *mccoyi* Whitley 1931, p. 311, 1940, p. 151, Victoria, Australia. But Fowler (1941, p. 278) who examined a specimen of *cookei* in Honolulu could not find "that *Echinorhinus cookei* is other than a variant of **brucus*", nor can we find anything in the accounts of *obesus* or of *mccoyi* to suggest that they differ significantly from **brucus,* as represented by a specimen of the latter from the eastern Atlantic in the British Museum (Bigelow and Schroeder 1948, Fig. 102), and by a male 1600 mm. long, from the coast of Mauritania, recently received through the kindness of Dr. A. M. Ramalho. On this basis, the recorded range of **brucus* includes the eastern North Atlantic from tropical West Africa to Ireland and the North Sea (including the Mediterranean); the coast of Massachusetts in the western North At-

lantic (one specimen found washed ashore at Provincetown, Massachusetts, in 1878); South Africa; Argentina; California; the Hawaiian, Japanese, and Australo-New Zealand regions, and Arabian waters. (For further details and for references, see Bigelow and Schroeder 1948, pp. 529-532.)

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PLATES

Plate 1. *Oxynotus centrina*. *Above*, lower surface of anterior part of head of female, 510 mm. long, coast of Portugal, x about 1.5. *Below*, roof of mouth of male, 590 mm. long, Portugal, viewed from below, to show arrangement of upper teeth, x about 6, both specimens Mus. Comp. Zool. No. 39576.

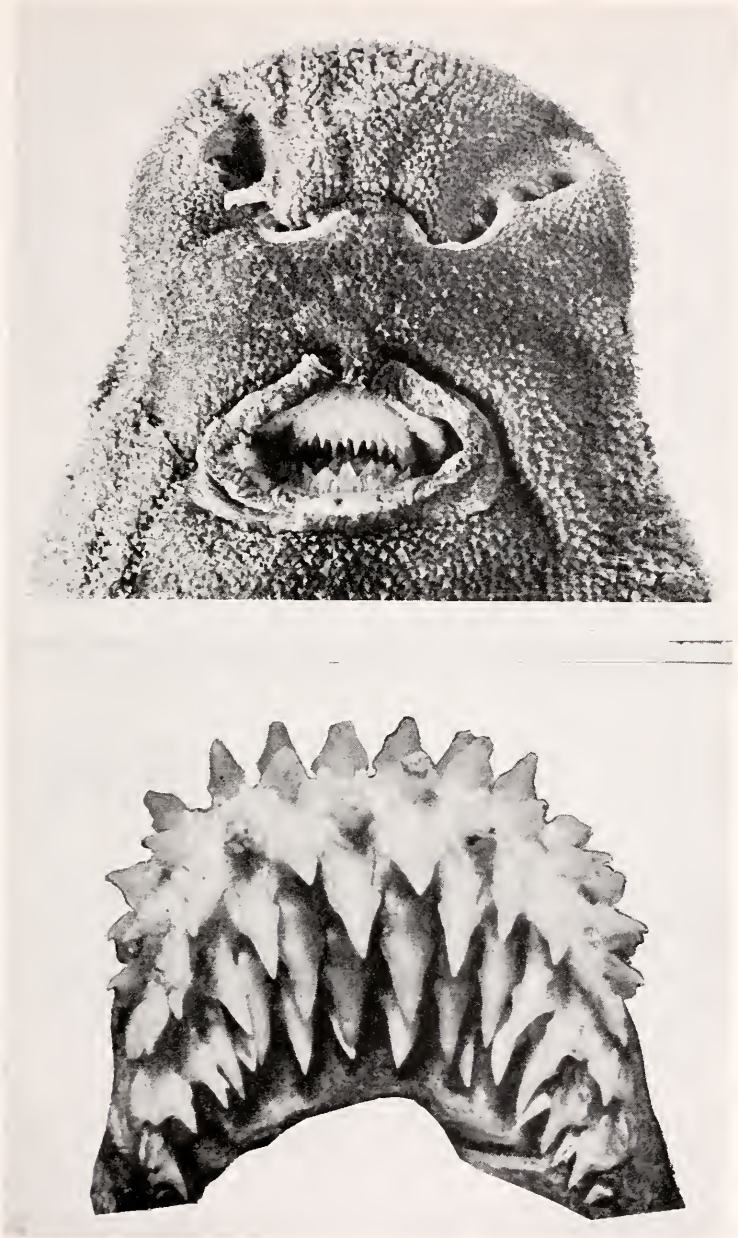

PLATE 1

Plate 2. *Etmopterus bullisi*, new species. Female, 196 mm. long, off northeast coast of Florida, Pelican sta. 42 (see p. 50). *Above*, side view of mid-sector of trunk, x about 3, to show the linear arrangement of the dermal denticles. *Below*, ventral view of same, at pectoral fins, to show the random arrangement of the denticles on the lower surface.

PLATE 2

Plate 3. *Above, Somniosus longus,* female 1010 mm. Mus. Comp. Zool. No. 39650, upper and lower teeth, left hand side of mouth, x about 3.3.

Middle and below, Somniosus microcephalus, upper and lower teeth, along central part of mouth, from jaws of a Gulf of Maine specimen about 11 feet long, Mus. Comp. Zool. No. 36119, x about 3.

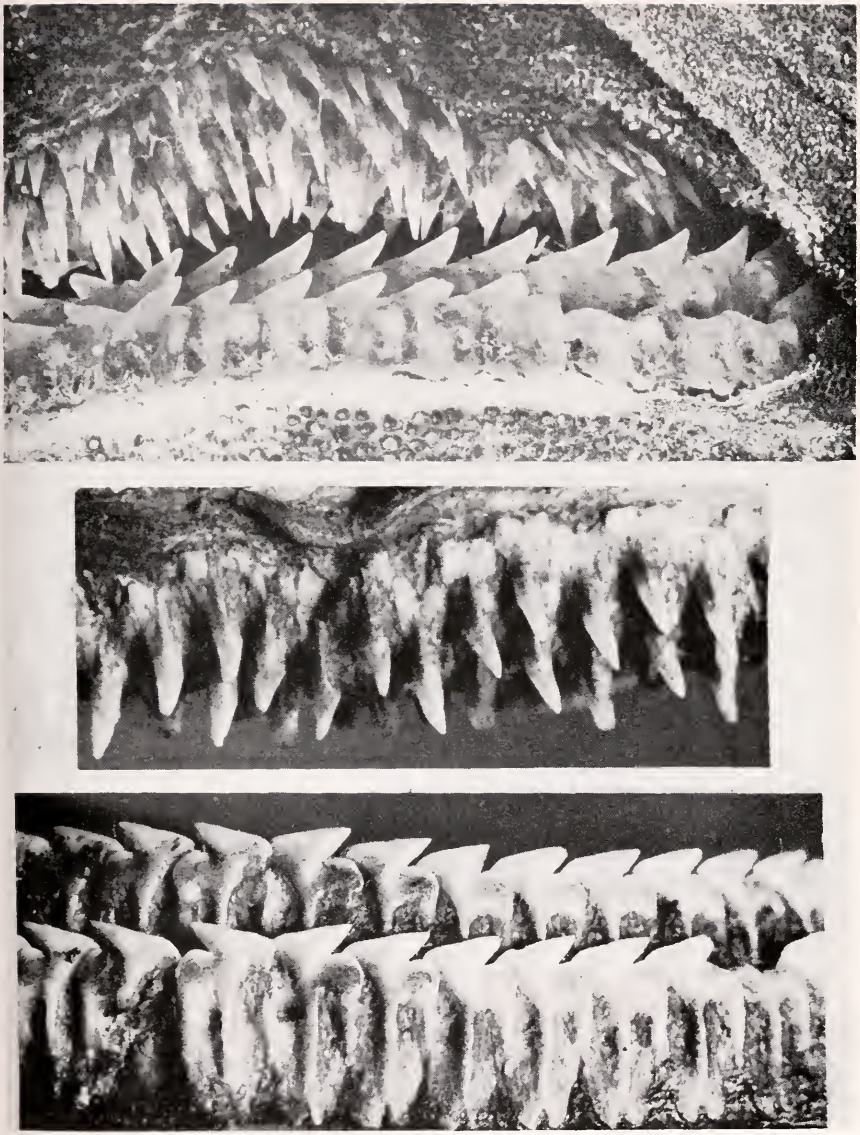

PLATE 3

Plate 4. *Above, Squaliolus laticaudus*, same specimen as in Figure 16A, photograph of mid-portion of trunk, to show papillate appearance of skin, x about 2.8.

Below, Euprotomicrus bispinatus, same specimen as in Figure 16F, corresponding photograph to show the smoothness of the skin as contrasted with *Squaliolus* (above), x about 3.

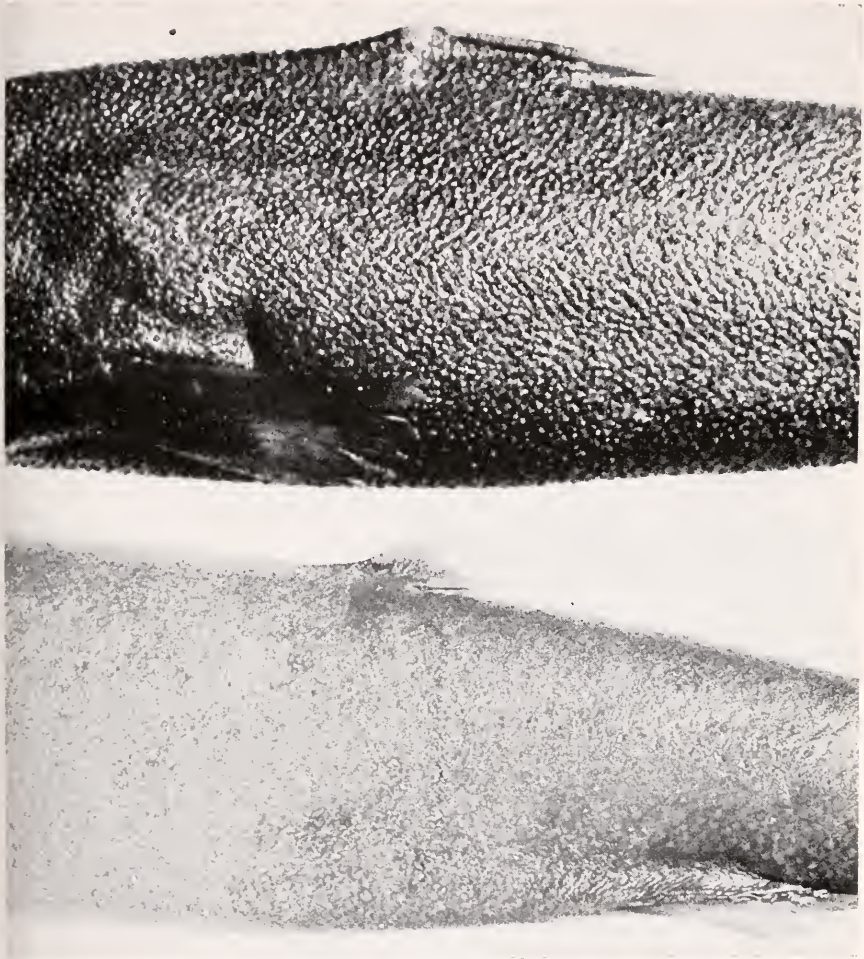

PLATE 4

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 117, No. 2

CHECK LIST OF THE REPTILES AND AMPHIBIANS OF EAST AFRICA (UGANDA; KENYA; TANGANYIKA; ZANZIBAR).

By Arthur Loveridge

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
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Proceedings of the New England Zoölogical Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 2. — *Check List of the Reptiles and Amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar)*

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INTRODUCTION

"A check list is the lowest class of literature." Though more profound observations have long since faded from memory, the preceding remark — made to me by a former colleague at the National Museum of Wales — has, strangely enough, never been forgotten. Possibly I was startled by G. R. Brook's dictum as the idea of a check list being considered as literature had never occurred to me. Nevertheless, however classified, a check list may serve a useful purpose in proportion to the time and care devoted to making it as free from error as may be humanly possible.

The present list owes its origin to a simple compilation of names extracted from such literature as was available to me in 1914, augmented by records of any specimens that had come my way. It was intended solely as a working basis for my personal use when I should reach East Africa. During the succeeding decade a number of additions resulted from my own field work. Upon my return from East Africa in 1923, I was urged by the then curator of reptiles at the British Museum, Dr. Joan B. Procter, to make it available to other workers.

Somewhat reluctantly I did so the following year, assuming I had seen the last of East Africa since I was proceeding to the United States. That check list, of which I never saw proof as it

was published in Kenya, certainly merited Brook's description. At that time, however, since it was the first list to cover the area, it was probably better than nothing!

The area covered was precisely the same as in the present list, viz:

Kenya Colony and Protectorate ..	224,960	square miles
Tanganyika Territory	360,000	" "
Uganda Protectorate	93,981	" "
Zanzibar Protectorate[1]	1,020	" "

Giving a total area of 679,961 square miles

It is, therefore, but little more than a quarter the size of the continental United States,[2] whose herpetofauna has been the subject of intensive study during the past century. East Africa, whose interior was largely a terra incognita sixty years ago, though only about a tenth of the area covered by the North American check list, straddles the equator. Consequently, though solely on an area basis, it enjoys a relatively richer herpetofauna, as shown by the following figures.

Group	Total number of forms listed as occurring in		
	East Africa in 1924[3]	East Africa in 1957	North America in 1953[4]
Turtles and Tortoises	13	15	81
Crocodilians	2	3	2
Lizards and Chameleons	155	179	148
Snakes	139	161	275
Amphibians	128	169	262
TOTALS	437	527	768

[1] Including Pemba Island with an area of approximately 380 square miles.

[2] 3,022,387 square miles which, added to that of Canada (3,695,189 square miles) gives a total of 6,717,576 for North America — the area covered by the 1953 check list.

As so many species are common to more than one territorial area, a regional breakdown of the new figures naturally results in some duplication. So far as Zanzibar Island is concerned, the situation remains obscured by the earlier use of the word Zanzibar (= Negro coast) in a broader sense that covered the mainland littoral of Tanganyika Territory only forty miles away. If only some resident naturalist would conduct a thorough survey of the island's herpetofauna, the matter might be cleared up once and for all. Though the figures for the three offshore islands correspond fairly closely to those of Moreau and Pakenham (1941: 109), actually a number of names have been dropped on account of synonymy or for other reasons, while others have been substituted or added.

Group	Uganda Protectorate	Kenya Colony	Tanganyika Territory	Pemba Island	Zanzibar Island	Mafia Island
Turtles and Tortoises	7	10	12	1	5	1
Crocodilians	2	1	2	0	1	0
Lizards and Chameleons	41	92	123	10	18	10
Snakes	69	89	113	9	33	12
Caecilians	0	3	7	0	0	0
Toads and Frogs	44	65	114	6	21	9
TOTALS	163	260	371	26	78	32

Apart from the inflation of the figures for Zanzibar's herpetofauna for the reasons given above, offset to some extent by the fact that the reptiles of its dependent island Pemba are little known, it is clear that there is a definite relation between speciation and area.

[3] The Amphibia are taken from a 1930 list published in the Proceedings of the Zoological Society of London, pp. 7-32.

[4] As no figures are given in the Check List of North American Amphibians and Reptiles, by K. P. Schmidt (ed. 6. University of Chicago Press), these are my own count in which are included the omitted forms in the addenda (1954, Copeia, pp. 304-306), but exclusive of recently introduced lizards (8 kinds) and frogs (3 forms).

At the time of the 1924 check list, when I arrived at the Museum of Comparative Zoology, that institution had only 161 of the 527 species and races now recognized. Today all but 33 are represented.

Number of listed forms represented in the Museum of Comparative Zoology				
Group	Present in 1923	Additions since 1924	Still lacking	Total
Turtles and Tortoises	11	4	0	15
Crocodilians	3	0	0	3
Lizards and Chameleons	49	121	9	179
Snakes	61	95	5	161
Caecilians	0	9	0	9
Toads and Frogs	37	104	19	160
TOTALS	161	333	33	527

Of this total of 527, I personally collected 413 in the field, while most of the remaining additions were obtained in exchange for duplicate material secured on the field trips I was privileged to carry out. The majority resulted from the itineraries being carefully planned to embrace not only type localities of our desiderata, but also type localities of many species or races that were inadequately described, or known only from one or two individuals. Topotypic series of these creatures resulted in 180 (73 + 107) alleged forms of reptiles and amphibians being relegated to the synonymy. Not always justifiably, though usually so. Nevertheless, anyone who proposes describing additions to the herpetofauna of East Africa, would be well advised to serutinize with care the synonyms attributed to the species most nearly related to the allegedly new form.

It is important to note the distinction between the names listed in the generic synonymies, and those of species or races. Following the citations for the 135 genera (110 of reptiles; 25 of amphibians) recognized in the present list, are 527 *additional*

citations. While the majority are straight synonyms, with a sprinkling of *nomina nuda,* others represent well-defined groups regarded by me as of subgeneric status. This is, of course, a matter of opinion, and to some of them a few of my fellow workers may wish to accord generic rank. Intensive study of any small group is apt to result in observed differences assuming an undue importance, at least temporarily. To adjust one's perspective it is advisable to evaluate the situation on a family basis.

In the 1924 check list no synonymies were supplied, so I trust their inclusion in the present one may serve a useful purpose. Is it too much to hope they may act as a deterrent to reckless describers like the late Ernst Ahl, of whose 95 "species" only 28 are considered valid? It is always possible that additional material may demonstrate that an occasional "synonym" represents a recognizable form, but "more material" is just as likely to have the opposite result. That 527 recognized forms should have 830 synonyms does not quite reflect the position, for more than half (274) have no synonyms whatever; on the other hand, several widely distributed species have a dozen or more each. It is but fair to say, however, that of these 1349[5] more or less useless names burdening the literature, not one was proposed by an African, but then neither was a single valid one!

This should not be construed as a reflection, for it is little more than a century since any one of the many indigenous tribes of the region had a written language. Not until 1848, I am informed, was the first of almost a hundred tongues in this area reduced to writing by a white immigrant. After all, following 300 years of civilizing contacts, it is doubtful whether an indigenous Indian described a single one of the 768 reptiles and amphibians that figure in the latest North American check list.

Genera. Chiefly for the benefit of herpetologists in Africa, working without benefit of library facilities, I have listed under each genus all of its synonyms known to me. After this check list was typed, I was given (through the courtesy of Dr. A. S. Romer) the opportunity to scan the extensive synonymies in an advance copy of his "Osteology of the Reptiles" (pp. xxi + 772: Chicago: 1956). This has enabled me to add between 20 and 30 synonyms of world-wide genera to the already lengthy lists. Gen-

[5] 527 generic + 822 species or races.

erally speaking, I have avoided inclusion of variations due to misprints or misspellings, together with some emendations (cf. footnote to *Chamaeleo* on p. 36. A few names that appear in the "Osteology" are omitted after due consideration. Unquestionably, further additions will have to be made in the case of wide-ranging genera with species in Europe or Asia.

Many tedious hours have been spent in attempting to ascertain the correct genotypes for each name. Where no type species had been mentioned I have occasionally selected one with the words "by present designation." Such action should be regarded as tentative, for in some instances further research may reveal that a type has already been proposed in some publication I have overlooked. Had I but realized at the outset how much time this uncongenial task would take I might well have shirked it, invoking the elder Agassiz's wise counsel to "Study specimens, not books." Sound advice which he apparently overlooked when, in compiling his "Nomenclature Zoologicus" (1842-1847), he proposed innumerable emendations in the spelling of generic names.

However, the chief offenders were Fitzinger and Gray who, apparently vying with each other in creating monotypic genera, have each proposed about 90 names — in so far as this list is concerned. Of these only 14 and 11 respectively are here regarded as full genera. Their percentages of validity (15% and 12%) compare very unfavorably with the more discriminating work of Günther (10 out of 31 valid) and of Peters (8 out of 24), each of whom achieved approximately 33 per cent.

Fitzinger, taking some work like the "Erpétologie Générale," gave Duméril and Bibron as the authors of his type species. As they in turn attributed the authorship to Linnaeus or some other early worker, I have cited the original author of the name with a view to avoiding much unnecessary printing. For example, in the case of *Psammorrhoa* Fitzinger (1843), instead of saying: "Type by original designation: *Agama aculeata* Duméril & Bibron = *Agama aculeata* Merrem," I have cited Merrem only, omitting Duméril & Bibron. I ask forgiveness of those taxonomically-minded colleagues who may be shocked by such action.

In the course of compiling these generic synonymies, I came across several names that had priority over those currently in use. Rulings setting aside these older names should be obtained from

the International Commission on Zoological Nomenclature without delay. They are:

Thermophilus Fitzinger (1843), not *Thermophila* Hübner (1816), antedates *Ichnotropis* Peters (1854) which has been in use as a genus of the LACERTIDAE for over a century.

Ibiba Gray (1825) antedates *Boiga* Fitzinger (part:1826), both having the same type: *Coluber irregularis* Merrem.

Cerastes Laurenti (1768), long associated with certain vipers, is quite unsuitable as a generic name for the docile opisthoglyphs currently known as *Psammophylax* Fitzinger (1843), both genera having the same type: *Coluber rhombeatus* Linnaeus.

Philodendros Fitzinger (1843), a most inappropriate name for the terrestrial snakes which have been known as *Dromophis* Peters (1869) for almost a century. Both genera have the same type: *Dendrophis praeornata* Schlegel.

Chloroechis Bonaparte (1849) antedates *Atheris* Cope (1862), a name that has been in use for almost a century. Both genera have the same type: *Vipera chloroechis* Schlegel.

At this point I might also mention *Cobra lachesis* Laurenti (1768). This is an earlier name for *Bitis a. arietans* Merrem (1820), the common Puff Adder which ranges from the Cape to Morocco. Some years ago *Cobra* was rejected as generically applicable. It is regrettable that *lachesis* was not dealt with at the same time, for reasons I have given elsewhere and have repeated briefly in a footnote to *arietans*.

Eminophis Werner (1924, Sitzb. Akad. Wiss. Wien, **133**, Abt. 1, p. 55), whose type (*E. lineolata* Werner) was said to have come from East Africa, was actually based on an Indian species — *Trachischum fuscum* (Blyth) — according to Malcolm A. Smith (1928, Ann. Mag. Nat. Hist., (10) **1**, p. 496).

Species and Races. The 1924 check list was largely binomial, only 7 "varieties" (of Boulengerian nomenclature) and 28 subspecies being cited. Of the 527 reptiles and amphibians figuring in this new list no fewer than 259 are expressed as trinomials — a change reflecting a better understanding of relationships and ranges. Several names appearing in the earlier list, or subsequently recorded from East Africa, have been omitted after an examination of the material on which they were based revealed misidentifications — usually of a subspecific nature. It is to be

hoped that they will not be reinstated by enthusiastic amateurs without due cause. Various species or races, rather too numerous to list, are now synonymized for the first time.

It will be observed that citations are given in a carefully standardized format. Precise date of publication is sometimes a problem. For example, it may be noted that the dates I give for many of the 34 species (common to East and South Africa) described by Sir Andrew Smith will be found to differ from those given by Boulenger in his catalogues. My dates were obtained from a paper by F. H. Waterhouse (1880, Proc. Zool. Soc. London, pp. 489-491), "On the Dates of Publication of the parts of Sir Andrew Smith's 'Illustrations of the Zoology of South Africa.'" The titles of some journals bear the name of the city of publication, e.g., Bull. Soc. Philom. Paris. Where omitted, and its absence may create difficulties, it has been added in parentheses, e.g., Bull. Mus. Hist. Nat. (Paris). Where a figure carries no number or letter, to show that it has not been inadvertently omitted I have expressed it thus: Fig. —.

It seems scarcely necessary to point out that capitals for specific or subspecific names are no longer in general use. Like hyphenated names they appear that way in the synonymy only when that was the way they were originally printed; for example, a specific name like *adolfifriderici* may have appeared as *Adolfi-friderici* in the first instance.

The description of *Gecko tuberculosus* Daudin (1802) seems to agree with the characters of the Common House-Gecko of East Africa long known as *Hemidactylus mabouia* (Moreau de Jonnés: 1818). However, the latter name having been in continuous use for 150 years, it is to be hoped a ruling to set *tuberculosus* aside will be secured from the International Commission on Zoological Nomenclature.

The only outstanding change meriting mention here is the use of *Boaedon fuliginosus fuliginosus* (Boie:1827) for the Common House-Snake, long known in East and South Africa as *Boaedon lineatus lineatus* Duméril & Bibron (1854). As the eastern reptile appears indistinguishable from the western, this vexatious change seems unavoidable.

Many extraterritorial species, even genotypes that are alien to Africa, are mentioned in footnotes or elsewhere. All are recorded

in the comprehensive *Index* which is the key to a mine of information that might be otherwise overlooked.

Ranges. In general, ranges are presented in a standardized format, the included countries — commencing with Spanish Morocco — being taken clockwise around the continent. Circumstances occasionally make deviations advisable as, for example where forest forms of western Kenya Colony extend due west to Gambia. Recent changes in political status such as Sudan (for the former Anglo-Egyptian Sudan), still differentiated by its spelling from the French Soudan, and Somalia (for Italian Somaliland) have been followed. Eritrea, however, though now merged with Ethiopia is faunistically so different that it appeared advisable to retain it as a separate entity. Other provinces that have been similarly treated are the huge units comprising the Union of South Africa, and sometimes it has seemed best to be specific with areas like the Gabon, instead of blanketing them in the vast region known as French Equatorial Africa. The territories comprising French West Africa also are at times listed individually.

When an animal occurs in any one of the four countries covered by this check list, that country is mentioned specifically. Though Mafia Island, lying south of Zanzibar, forms part of Tanganyika Territory, zoogeographically it is simpler to list it along with Pemba and Zanzibar Islands, from whose sultanate it was once administered. The word "coastal" is employed to denote the lowland zone extending from the Indian Ocean to the continental plateau. In width it varies considerably for a dozen degrees south of the equator. Its characteristic herpetofauna reaches inland as far as Lake Nyasa and even beyond.

It need hardly be pointed out that the ranges furnished are only as of 1956, and subject to extension as our knowledge increases. Caution should be exercised in extending them to include improbable records, for the distribution of many species is conditioned by well-defined habitat preferences. The nine principal faunal zones have been discussed elsewhere (Loveridge, 1937, Bull. Mus. Comp. Zool., **79**, pp. 481-541), and the majority of species in this check list assigned to one or more of the zones.

Our understanding of *Hyperolius* is so far from complete that to avoid misunderstandings as to the ranges of these sedge- or

tree-frogs I have departed from the format employed elsewhere by indicating with an asterisk (*) precisely those countries from which material of the particular species or race is present in the collections of the Museum of Comparative Zoology. As a further safeguard, countries included on the basis of unique records are followed, in parentheses, by the name of the responsible authority and the year in which he published the record. This procedure has also been used for members of the RANIDAE.

Footnotes. Primarily for the benefit of isolated workers in Africa, explanatory annotations have been given in the form of footnotes. These provide references to, or the reasons for, relatively recent taxonomic changes; others are intended to elucidate ambiguities or to account for seeming omissions, especially where due to erroneous records. A few refer to unsolved problems and indicate profitable lines of investigation that need to be undertaken.

ACKNOWLEDGEMENTS

The policy of submitting a check list, prior to publication, to the scrutiny of one's colleagues is an admirable one. Unfortunately, most of those interested in African herpetology are overseas, besides which the time factor militates against putting the idea into practice in this instance. However, help has been received from various correspondents and colleagues, and I welcome this opportunity of expressing my deep appreciation for their assistance. My thanks go to: Mr. J. C. Battersby of the British Museum for his kindness in answering sundry questions. Dr. O. G. S. Davis of Purdue University for allowing me to see her manuscript synonymy of *Python* and *Eryx*. Dr. V. F. FitzSimons of the Transvaal Museum for information regarding certain South African amphibia, and early type localities not to be found on recent maps. Dr. Carl Gans of Harvard University for rectifying my concept of the genus *Dasypeltis* and permitting me to use his amended synonymy. Mons. Jean Guibé of the Muséum National d'Histoire Naturelle for examining the Kenya specimen of *Bufo latifrons*. Henry Horn of Cambridge High and Latin School for his conscientious and painstaking work in checking citations, arranging the vast index, and related matters. C. J. P. Ionides, Esq., of Tanganyika Territory, whose

fine field work has added several new species to East Africa's herpetofauna, and extended the known ranges of others. Miss J. B. MacKenzie and her staff in the library of the Museum of Comparative Zoology, for their ever willing help and skill in tracking down references to obscure or inadequately cited publications. Dr. Ernst Mayr of this museum for advice on various knotty problems of a taxonomic nature. Dr. Robert Mertens of Senckenberg Museum for answering questions respecting early German publications and Boettger types. Dr. H. W. Parker of the British Museum for sundry information, and for pin-pointing obscure localities in Ethiopia and Somalia. Mr. Benjamin Shreve, my colleague for the past twenty-five years, for friendly advice as to the gender and correct suffixes of sundry scientific names. Dr. M. A. Smith of the British Museum for scanning the pages relating to the synonymy of the HYDROPHIIDAE. Dr. E. E. Williams of Harvard University for examining the dentition of *Cacosternum*, and other favours. It is from our recently published revision of the CRYPTODIRA that the synonymy of the East African members of that suborder have been taken. Miss N. E. Wright of this museum for her painstaking editorship of this manuscript.

Class REPTILIA

Subclass ANAPSIDA

Order TESTUDINATA[6]

Suborder CRYPTODIRA[7]

Family DERMOCHELYIDAE

Genus **DERMOCHELYS** Blainville

1816. *Dermochelys* Blainville, Bull. Soc. Philom. Paris, p. "111" (mis-

[6] The oldest name for the entire group is TESTUDINES Batsch, 1788 (Anleit. Kennt. Thiere Mineral, 1, p. 437), rejected as being merely a nominative plural of *Testudo*. CHELONIA Macartney, 1802 (in Ross, Transl. Cuvier, List. Comp. Anat. 1, pl. iii) is discarded as likely to result in confusion with the genus *Chelonia* and with adjectives derived therefrom. Consequently, as the laws of priority are not applicable to ordinal names, TESTUDINATA Oppel, 1811 (Ordn. Rept., p. 3) is preferred.

[7] Other suborders of TESTUDINATA are used by some herpetologists. On account of its peculiar carapacial structure they would isolate *Dermochelys* as suborder ATHECAE, all other turtles and tortoises being grouped under THECOPHORA. Such a separation has been considered undesirable by some anatomists and other recent workers.

print = 119). Type by monotypy: *Testudo coriacea* Linnaeus.

1820. *Sphargis* Merrem, Vers. Syst. Amphib., p. 19. Type by monotypy: *Testudo coriacea* Linnaeus.

1822. *Coriudo* Fleming, Phil. Zool., **2**, p. 271. Type by monotypy: *Testudo coriacea* Linnaeus.

1828. *Scytina* Wagler, Isis von Oken, **21**, col. 861. Substitute name for *Sphargis* Merrem.

1830. *Dermatochelys* Wagler, Nat. Syst. Amphib., p. 133. Emendation for *Dermochelys*.

1832. *Chelyra* Rafinesque, Atlantic Journ., **1**, p. 64. Type by monotypy: *Testudo coriacea* Linnaeus.

Dermochelys coriacea (Linnaeus) Luth or Leathery Turtle

1766. *Testudo coriacea* Linnaeus, Syst. Nat., ed. 12, **1**, p. 350: Mediterranean Sea.

1771. *Testudo arcuata* Catesby, Nat. Hist. Carolina, **2**, p. 40: Coasts of Carolina and Florida (by inference).

1788. *Testudo lyra* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, Synopsis Methodica (also p. 111 as *Le Luth*): Barbary Coast, North Africa.

1792. *Testudo tuberculata* Schoepff, Hist. Testud., p. 144: No locality.

1814. *Chelonia lutaria* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66: Mediterranean Sea.

1820. *Sphargis mercuralis* Merrem, Vers. Syst. Amphib., p. 19: Mediterranean Sea and Atlantic Ocean.

1829. *Dermochelis Atlantica* Lesueur (*nomen nudum*), in Cuvier, Règne Animal, ed. 2, **2**, p. 14, footnote: No locality.

1830. *Dermatochelys porcata* Wagler, Nat. Syst. Amphib., pl. i, figs. 1-23 (on p. 133 *coriacea* is used): No locality.

1884. *Sphargis coriacea* var. *Schlegelii* Garman, U. S. Nat. Mus. Bull. No. 25, pp. 295, 303: Tropical Pacific and Indian Oceans.

1899. *Sphargis angusta* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 730, pl. i: Tocopilla, Chile.

Range. Indian and other tropical oceans, and, as an accidental visitor, the temperate seas.

Family CHELONIIDAE

Genus **CHELONIA** Brongniart

1800. *Chelonia* Brongniart (part), Bull. Soc. Philom. Paris, **2**, p. 89. Type designated by Fitzinger:1843: *Testudo mydas* Linnaeus.

1837. *Chelona* Burmeister, Handbuch Naturg., **2**, Abt. Zool., p. 731. Type by monotypy: *Testudo mydas* Linnaeus.

1838. *Mydas* Cocteau (not Fabricius:1799), Rept., in Sagra, Hist. Fis.

Pol. Nat. Cuba, **4**, p. 22. Type by tautonomy: *Testudo mydas* Linnaeus.

1843. *Mydasea* Gervais, Dict. Hist. Nat., **3**, p. 457. Type by tautonomy: *Testudo mydas* Linnaeus.

1845. *Euchelonia* Tschudi, Fauna Peruana, Herp., p. 22. Type by monotypy: *Testudo mydas* Linnaeus.

1848. *Megemys* Gistel, Naturg. Thierr., p. viii. Substitute name for *Chelonia* Brongniart.

1858. *Euchelys* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 447. Type by monotypy: *E. macropus* Girard = *Testudo mydas* Linnaeus.

1862. *Chelone* Strauch, Mém. Acad. Imp. Sci. St.-Pétersbourg, (7) **5**, No. 7, p. 59. Type by original designation: *Testudo viridis* Schneider = *T. mydas* Linnaeus.

Chelonia mydas (Linnaeus) Green Turtle

1758. *Testudo mydas* Linnaeus, Syst. Nat., ed. 10, **1**, p. 197: Ascension Island.

1782. *Testudo* (*macropus*) Walbaum, Chelongr. Schildkröten, p. 112: No locality.

1783. *Testudo Viridis* Schneider, Natur. Schildkröten, p. 299: No locality.

1787. *Testudo japonica* Thunberg, Vetensk. Acad. Handl., **8**, p. 178, pl. vii, fig. 1: Japan.

1788. *Testudo marina* (seu *vulgaris*) Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, Synopsis Methodica (also p. 54 as *La Tortue Franche*): Torrid Zone.

1788. *Testudo viridis-squamosa* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, Synopsis Methodica (also p. 92 as *La Tortue écaille-verte*): Amazon River, Brazil.

1802. *Testudo cepediana* Daudin, Hist. Nat. Rept., **2**, p. 50, pl. xvii, fig. 1: No locality.

1812. *Chelonia virgata* Schweigger, Konigsberger Arch. Naturwiss. Math., **1**, pp. 291, 334, 411: Seas of the Torrid Zone.

1820. *Caretta esculenta* Merrem, Vers. Syst. Amphib., p. 18: Atlantic Ocean.

1820. *Caretta nasicornis* Merrem, Vers. Syst. Amphib., p. 18: Ocean near America.

1820. *Caretta Thunbergii* Merrem, Vers. Syst. Amphib., p. 19: Japan.

1829. *Chelonia maculosa* Cuvier, Règne Animal, ed. 2, **2**, p. 13: No locality.

1829. *Chelonia lachrymata* Cuvier, Règne Animal, ed. 2, **2**, p. 13: No locality.

1834. *Chelonia bicarinata* Lesson, in Bélanger, Voy. Indies-Orient., Zool., p. 301: Atlantic Ocean.

1835. *Chelonia Marmorata* Duméril & Bibron, Erpét. Gén., **2**, p. 546, pl. xxiii, fig. 1: Ascension Island.
1858. *Chelonia formosa* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 456, pl. xxxi, figs. 1-4: Fiji Islands.
1858. *Chelonia tenuis* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 459, pl. xxxi, fig. 8: Honden Island, Paumotu Group, Tahiti and Eimeo; Rosa Island.
1868. *Chelonia Agassizii* Bocourt, Ann. Sci. Nat. Zool. (Paris), (5) **10**, p. 122: Nagulate River mouth, Guatemala.
1880. *Chelonia depressa* Garman (at least in part), Bull. Mus. Comp. Zool., **6**, p. 124: East Indies (juvenile).
1887. *Chelonia lata* Philippi, Zool. Garten, **28**, p 84: near Valparaiso, Chile.

Range. Indian and other tropical oceans and, as an accidental visitor, the temperate seas.

Genus **ERETMOCHELYS** Fitzinger

1828. *Caretta* Ritgen (not Rafinesque:1814), Nova Acta Acad. Leop.-Carol., **14**, p. 270. Type by monotopy: *Testudo imbricata* Linnaeus.
1843. *Eretmochelys* Fitzinger, Syst. Rept., p. 30. Type by original designation: *Testudo imbricata* Linnaeus.
1868. *Herpysmostes* Gistel in Blicke, Leben Natur Menschen (Leipzig), p. 145. Type (*fide* Mertens:1936): *Testudo imbricata* Linnaeus.
1873. *Onychochelys* Gray, Proc. Zool. Soc. London, p. 397, figs. 1-2. Type by monotypy: *O. kraussi* Gray = *Testudo imbricata* Linnaeus.

Eretmochelys imbricata (Linnaeus) Hawksbill Turtle

1766. *Testudo imbricata* Linnaeus, Syst. Nat., ed. 12, **1**, p. 350: American and Asiatic seas.
1834. *Chelonia pseudo-mydas* Lesson, in Bélanger, Voy. Indies-Orient., Zool., p. 299: Atlantic Ocean.
1834. *Chelonia pseudo-caretta* Lesson, in Bélanger, Voy. Indies-Orient., Zool., p. 302: Atlantic Ocean.
1835. *Caretta Bissa* Rüppell, Neue Wirbelth. Fauna Abyssinica, Amphib., p. 4, pl. ii: Red Sea.
1857. *Eretmochelys squamata* Agassiz, Contr. Nat. Hist. U. S., **1**, p. 382: Indian and Pacific Oceans.
1858. *Caretta squamosa* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 442, pl. xxx, figs. 1-7: Sulu Seas and Indian Ocean.
1858. *Caretta rostrata* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 446, pl. xxx, figs. 8-13: Fiji Islands.
1873. *Onychochelys kraussi* Gray, Proc. Zool. Soc. London, p. 398, figs. 1-2: Atlantic Ocean off French Guiana.

Range. Indian and other tropical oceans and, as an accidental visitor, the temperate seas.

Genus **CARETTA** Rafinesque

1814. *Caretta* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66. Type by monotypy: *C. nasuta* Rafinesque = *Testudo caretta* Linnaeus.

1835. *Thalassochelys* Fitzinger, Ann. Wiener Mus., **1**, pp. 110, 121, 128. Type by original designation: *T. caouana* Fitzinger = *Testudo caretta* Linnaeus.

1838. *Caouana* Cocteau, Rept., in Sagra, Hist. Fis. Pol. Nat. Cuba, **4**, p. 31. Type by monotypy: *Thalassochelys cephalo* Schneider = *Testudo caretta* Linnaeus.

1843. *Halichelys* Fitzinger, Syst. Rept., p. 30. Type by original designation: *H. atra* Fitzinger = *Testudo caretta* Linnaeus.

1873. *Cephalochelys* Gray, Proc. Zool. Soc. London, p. 408. Type by monotypy: *C. oceanica* Gray = *Testudo caretta* Linnaeus.

1873. *Eremonia* Gray, Proc. Zool. Soc. London, p. 408. Type by monotypy: *E. elongata* Gray = *Testudo caretta* Linnaeus.

Caretta caretta (Linnaeus) Red-brown Loggerhead

1758. *Testudo Caretta* Linnaeus, Syst. Nat., ed. 10, **1**, p. 197: Islands off America.

1783. *Testudo Cephalo* Schneider, Natur. Schildkröten, p. 303: No locality.

1788. *Testudo caouana* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, Synopsis Methodica (also p. 95 as *La Caouane*): Jamaica, British West Indies (restricted).

1788. *Testudo nasicornis* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, Synopsis Methodica (also p. 103 as *La Tortue nasicorne*): America.

1814. *Caretta nasuta* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66: Sicily (*fide* Lindholm:1929).

1820. *Caretta atra* Merrem, Vers. Syst. Amphib., p. 17: Ascension Island.

1833. *Chelonia pelasgorum* Valenciennes, pl. vi, in Bory, Expéd. Sci. Morée, Zool.: Modon, etc., Mediterranean Sea.

1844. *Caouana elongata* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 53: No locality.

1858. *Thalassochelys corticata* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 431, pl. xxix: Madeira Islands.

1873. *Cephalochelys oceanica* Gray, Proc. Zool. Soc. London, p. 408: Mexico.

1887. *Thalassochelys tarapacona* (*sic*) Philippi (identified by subsequent

description of Philippi:1899), Zool. Garten, **28**, p. 85: Iquique, Chile.

1930. *Caretta gigas* Deraniyagala, Ceylon Journ. Sci., (B), **18**, p. 66, figs. 4-6, pl. v: Gulf of Mannar, Ceylon.

Range. Indian and other tropical oceans and, as an accidental visitor, the temperate seas.

Genus **LEPIDOCHELYS** Fitzinger

1843. *Lepidochelys* Fitzinger, Syst. Rept., p. 30. Type by original designation: *Chelonia olivacea* Eschscholtz.

1880. *Colpochelys* Garman, Bull. Mus. Comp. Zool., **6**, p. 124. Type by monotypy: *C. kempi* Garman.

Lepidochelys olivacea olivacea (Eschscholtz)

Olive Loggerhead

1820. ?*Chelonia multiscutata* Kuhl, Beitr. Zool. Anat., **1**, p. 78: No locality.

1829. *Chelonia olivacea* Eschscholtz, Zool. Atlas, p. 3, pl. iii: Manila Bay, Philippine Islands.

1835. *Chelonia Dussumierii* Duméril & Bibron, Erpét. Gén., **2**, p. 557, pl. xxiv, figs. 1-1a: China Sea and Malabar Coast.

1844. *Caouana Rüppellii* Gray (*nomen nudum*), Cat. Tort. Croc. Amphis. Brit. Mus., p. 53: India?

1857. *Chelonia polyaspis* Bleeker, Nat. Tijdschr. Ned. Indies, **14**, p. 239: Batavia, Java.

1889. *Chelonia dubia* Bleeker (*nomen nudum*), in Boulenger, Cat. Chelon. Rhyncho. Croc. Brit. Mus., p. 186: Borneo.

1899. *Thalassochelys controversa* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 732: No locality.

1908. *Caretta remivaga* Hay, Proc. U. S. Nat. Mus., **34**, p. 194, pl. x, figs. 1-3; pl. xi, fig. 5: Ventosa Bay, Gulf of Tehuantepec, Mexico.

Range. Indian and other tropical oceans and, as an accidental visitor, the temperate seas.

Family TESTUDINIDAE

Genus **TESTUDO** Linnaeus[8]

1758. *Testudo* Linnaeus, Syst. Nat., ed. 10, **1**, p. 197. Type by subsequent designation of Fitzinger: *Testudo graeca* Linnaeus.

[8] In place of the single genus *Testudo* some authorities would recognize several full genera (*Testudo; Geochelone; Psammobates*). Despite possibly ancient separation I personally prefer to regard these groups as of only subgeneric rank. However, this is merely my personal opinion; for those who think otherwise and consider *Geochelone* as a full genus, the only synonyms of it would be *Centrochelys; Stigmochelys* and *Megachersine*.

1820. *Chersine* Merrem, Vers. Syst. Amphib., pp. 12, 29. Type by subsequent designation of Lindholm: *Testudo graeca* Linnaeus.

1830. *Chersus* Wagler, Nat. Syst. Amphib., p. 138. Type by monotypy: *Testudo marginata* Schoepff.

1835. *Psammobates* Fitzinger, Ann. Weiner Mus., **1**, pp. 108, 113, 122. Type by original designation: *Testudo geometrica* Linnaeus.

1835. *Geochelone* Fitzinger, Ann. Weiner Mus., **1**, pp. 111, 112, 122. Type by original designation: *Testudo stellata* Schweigger = *T. elegans* Schoepff.

1869. *Peltastes* Gray (not Rossi:1807), Proc. Zool. Soc. London, pp. 167, 171. Type by subsequent designation of Lindholm: *Testudo graeca* Linnaeus.

1870. *Chersinella* Gray, Suppl. Cat. Shield Rept. Brit. Mus., part 1, p. 8. Type by subsequent designation of Lindholm: *Testudo gracca* Linnaeus.

1870. *Testudinella* Gray (not Bory:1826), Suppl. Cat. Shield Rept. Brit. Mus., part 1, p. 12. Type by monotypy: *Testudo horsfieldi* Gray.

1872. *Peltonia* Gray, App. Cat. Shield Rept. Brit. Mus., p. 4. New name for *Peltastes* Gray (preoccupied).

1872. *Centrochelys* Gray, App. Cat. Shield Rept. Brit. Mus., p. 5. Type by monotypy: *Testudo sulcata* Miller.

1873. *Stigmochelys* Gray, Hand-List Shield Rept. Brit. Mus., p. 5. Type by monotypy: *Testudo pardalis* Bell.

1916. *Medaestia* Wussow, Wochenschr. Aquar.-Terrar. Kunde, **13**, p. 170. Type by subsequent designation of Mertens: *Testudo graeca* Linnaeus.

1933. *Megachersine* Hewitt, Ann. Natal Mus., **7**, p. 257. Type by original designation: *Testudo pardalis* Bell.

1933. *Chersinella* Hewitt (not Gray:1870), Ann. Natal Mus., **7**, p. 259. Type by original designation: *Testudo geometrica* Linnaeus.

Testudo pardalis babcocki Loveridge Eastern Leopard Tortoise

1935. *Testudo pardalis babcocki* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 4: Mount Debasien, Karamojo, Uganda.

Range. Sudan and Ethiopia, south through Uganda; Kenya Colony and Tanganyika Territory to Natal, west through Cape Province to Southwest Africa where it meets with the typical form, but is dominant north of 25° S. and in southern Angola.

Genus **MALACOCHERSUS** Lindholm

1929. *Malacochersus* Lindholm, Zool. Anz., **81**, p. 285. Type by original designation: *Testudo tornieri* Siebenrock.

Malacochersus tornieri (Siebenrock) Pancake Tortoise

1903. *Testudo tornieri* Siebenrock, Anz. Akad. Wiss. Wien, **40**, p. 185: Busisi, Smith Sound, Lake Victoria, Tanganyika Territory.

1920. *Testudo Loveridgii* Boulenger, C. R. Acad. Sci. (Paris), **170**, p. 263: Dodoma, Ugogo, Tanganyika Territory.

1923. ?*Testudo procterae* Loveridge, Proc. Zool. Soc. London, p. 298, pls. i-ii: Ikikuyu, south of Gulwe, Tanganyika Territory.[9]

Range. Rocky hills of Kenya Colony (Mathews Range south to Njoro, east to Midas Creek), and Tanganyika Territory (from Busisi, Smith Sound, southeast through Ugogo to Lindi).

Genus **KINIXYS** Bell

1827. *Kinixys* Bell, Trans. Linn. Soc. London, **15**, p. 398. Type by original designation: *K. castanea* Bell = *Testudo erosa* Schweigger.

1835. *Cinothorax* Fitzinger, Ann. Wiener Mus., **1**, pp. 108, 111, 121. Type by subsequent designation of Fitzinger:1843: *Kinixys belliana* Gray.

1843. *Cinixys* Fitzinger, Syst. Rept., p. 29. Emendation for *Kinixys* Bell.

1873. *Kinothorax* Gray, Hand-List Shield Rept. Brit. Mus., p. 16. Emendation for *Cinothorax* Fitzinger.

Kinixys belliana belliana Gray Bell's Eastern Hinged-Tortoise

1831. *Kinixys Belliana* Gray, Synopsis Reptilium, p. 69: No locality. ("W. Africa ?", later added by Boulenger, appears doubtful.)

1845. *Kinixys schoensis* Rüppell, Mus. Senckenberg., **3**, p. 226, pl. xvi, figs. 1-3: Shoa, southern Ethiopia.

1863. *Kinixys Spekii* Gray, Ann. Mag. Nat. Hist., (3) **12**, p. 381: "Central Africa" (probably northwest Tanganyika Territory).

1902. *Homopus darlingi* Boulenger, Proc. Zool. Soc. London, **2**, p. 15, pl. iv: Salisbury District, Mashonaland, Southern Rhodesia.

1927. *Cinixys lobatsiana* Power, Trans. Roy. Soc. S. Africa, **14**, p. 410, pls. xix-xx: Lobatsi, Bechuanaland Protectorate.

1931. *Kinixys belliana zombensis* Hewitt, Ann. Natal Mus., **6**, p. 469, fig. 1c, pl. xxxviii, fig. 4: Zomba, Nyasaland.

1931. *Kinixys belliana zuluensis* Hewitt, Ann. Natal Mus., **6**, p. 471, figs. 1a-1b, pl. xxxviii, figs. 1-3, 5-10: Richard's Bay, Zululand.

1931. *Kinixys australis* Hewitt, Ann. Natal Mus., **6**, p. 477, pl. xxxvi, figs. 4-6: White River, Nelspruit, Lydenburg District, Transvaal.

[9] As Procter's Soft-shelled Land-Tortoise is known only from a single specimen, it is tentatively relegated to the synonymy on geographical grounds until someone can secure a series from the type locality, which should not be confused with the Ikikuyu just outside Dodoma. Not only is *M. procterae* strikingly different in coloration from every one of the more than a hundred *tornieri* I have seen, but also its head scalation, especially its large and elongate prefrontals, is unique.

1931. *Kinixys jordani* Hewitt, Ann. Natal Mus., **6**, p. 481, pl. xxxvii, figs. 7-9 (*not* 1-3 as stated): Isoka, Northern Rhodesia.

1931. *Kinixys youngi* Hewitt, Ann. Natal Mus., **6**, p. 486, fig. 1d, pl. xxxvii, figs. 4-5: Lake Nyasa shore below Livingstonia, Nyasaland.

1932. *Kinixys australis mababiensis* FitzSimons, Ann. Transvaal Mus., **15**, p. 37: Tsotsoroga Pan, Mababe Flats, Bechuanaland Protectorate.

1935. *Kinixys natalensis* Hewitt, Rec. Albany Mus., **4**, p. 353, pl. xxxv, figs. 3-4: Jameson's Drift, Tugela River Valley, Natal.

Range. Eritrea southwest to Natal, northwest through Bechuanaland and Angola to French Cameroon where it meets with the western race (which has only four claws on forelimb). Madagascar.

Kinixys erosa (Schweigger) Western-Forest Hinged-Tortoise

1812. *Testudo erosa* Schweigger, Konigsberger Arch. Naturwiss. Math., **1**, p. 321: "America septentrionali" (error).

1826. *Testudo Schöpfii* Fitzinger (*nomen nudum*), Neue Class. Rept., p. 44: No locality.

1827. *Kinixys castanea* Bell, Trans. Linn. Soc. London, **15**, p. 398, pl. xvii, fig. 1: Africa.

Range. Uganda, west through the Belgian Congo to Gambia.

Family TRIONYCHIDAE

Genus **TRIONYX** Geoffroy[10]

1809. *Trionyx* Geoffroy Saint-Hilaire, Ann. Mus. Hist. Nat. (Paris), **14**, p. 1. Type by original designation: *T. aegyptiacus* Geoffroy = *Testudo triunguis* Forskål.

1830. *Aspidonectes* Wagler, Nat. Syst. Amphib., p. 134. Type by designation of Stejneger: *Trionyx aegyptiacus* Geoffroy = *Testudo triunguis* Forskål.

1835. *Gymnopus* Duméril & Bibron, Erpét. Gén., **2**, p. 472. New name for *Aspidonectes* Wagler.

1844. *Tyrse* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 47. Type by tautonomy: *Trionyx nilotica* Gray = *Testudo triunguis* Forskål.

1869. *Fordia* Gray, Proc. Zool. Soc. London, p. 219. Type by monotypy: *F. africana* Gray = *Testudo triunguis* Forskål.

[10] Only synonyms based on African species are given here as it seems scarcely worth while to list the 24 additional ones involving American and Asiatic species. These can be found in the recently published revision of African Cryptodira (see Bibliography).

Trionyx triunguis (Forskål) Nile Soft-shelled Turtle

1775. *Testudo triunguis* Forskal, Descr. Anim. Avium, Amphib., p. ix: Nile, Egypt.

1809. *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, Ann. Mus. Hist. Nat. (Paris), **14**, p. 12, pls. i-ii: Nile, Egypt.

1831. *Trionyx Niloticus* "Shaw" Gray, Synopsis Reptilium, p. 46: Nile, Egypt.

1837. *Trionyx labiatus* Bell, Monog. Testudinata, text to pls. — (= xviii-xx): Sierra Leone.

1844. *Trionyx Mortoni* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 120: Africa.

1859. *Aspidonectes aspilus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 295: Ovenga and Rembo Rivers, Fernan Vaz, French Congo.

1869. *Fordia africana* Gray, Proc. Zool. Soc. London, p. 219: Nile River at Khartoum, Sudan.

1948. *Trionyx triunguis rudolfianus* Deraniyagala, Spolia Zeylanica (Colombo), **25**, 2, p. 30, fig. 5, pl. xii, fig. c: Ferguson's Gulf, Lake Rudolf, Kenya Colony.

Range. Egypt and Eritrea south to Lake Rudolf, Kenya Colony; southwest to Lake Albert, Uganda; and Angola; northwest to Senegal. Accidental visitor along the Palestine coast of Asia Minor.

Genus **CYCLODERMA** Peters

1854. *Cycloderma* Peters, Monatsb. Akad. Wiss. Berlin, p. 216. Type by monotypy: *C. frenatum* Peters.

1856. *Cryptopodus* A. Duméril, Revue Mag. Zool. (2), **8**, p. 374. Lapsus for *Cryptopus* Duméril & Bibron = *Cyclanorbis* (part).

1859. *Heptathyra* Cope, Proc. Nat. Sci. Philadelphia, p. 294. Type by monotypy: *Cryptopus* (*sic*) *aubryi* A. Duméril.

1860. *Aspidochelys* Gray, Proc. Zool. Soc. London, p. 6. Type by monotypy: *A. livingstonii* Gray = *Cycloderma frenatum* Peters.

Cycloderma frenatum Peters Zambezi Soft-shelled Turtle

1854. *Cycloderma frenatum* Peters, Monatsb. Akad. Wiss. Berlin, p. 216: Zambezi River, Mozambique.

1860. *Aspidochelys livingstonii* Gray, Proc. Zool. Soc. London, p. 6, pl. xxii, figs. 1-2: Tributaries of Zambezi, Mozambique.

Range. Southern Tanganyika Territory, west and south through Nyasaland (and possibly Northern Rhodesia) to Mozambique.

Suborder PLEURODIRA

Family PELOMEDUSIDAE

Genus **PELOMEDUSA** Wagler

1830. *Pelomedusa* Wagler, Nat. Syst. Amphib., p. 136. Type by monotypy: *Testudo galeata* Schoepff = *Testudo subrufa* Lacépède.

1835. *Pentonyx* Duméril & Bibron, Erpét. Gén., **2**, p. 389. Type by subsequent designation: *P. capensis* Duméril & Bibron = *Testudo subrufa* Lacépède.

Pelomedusa subrufa olivacea (Schweigger)[11]

Northern Marsh-Terrapin

1814. *Emys olivacea* Schweigger, Prodromi Mon. Chelon., p. 38: "In Fabulosis Nigritae," as Adanson coll. = Senegal.

1835. *Pentonyx Gehafie* Rüppell, Neue Wirbelth. Fauna Abyssinica, Amphib., p. 2, pl. 1: Massaua, Eritrea.

1884. *Pelomedusa Gasconi* Rochebrune, Faune Senegambie, Rept., p. 25, pl. i, figs. 1-2: Dagana, Senegal (restricted).

1910. ?*Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, Hist. Phys. Nat. Pol. Madagascar, **17**, Rept., p. 56, pl. xx, fig. 3: Du Bourg de Bozas coll., but no locality.

Range. Uncertain, but apparently a northern belt extending from Senegal to Eritrea and intergrading with the typical form in northern Uganda and northern Kenya Colony with occasional individuals cropping up in the south and Madagascar.

Pelomedusa subrufa subrufa (Lacépède)

Southern Marsh-Terrapin

1788. *Testudo subrufa* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, Synopsis Methodica (also p. 173 as *La Roussatre*): "de L'Inde," as collected by Sonnerat restricted to Cape of Good Hope, South Africa.

1792. *Testudo galeata* Schoepff, Hist. Testud., p. 12, pl. iii, fig. 1: "India orientale, Carolina," restricted to Cape Flats, Cape Province, South Africa.

1798. *Testudo Badia* Donndorf, Zool. Beytrage Linn. Natur., **3**, p. 34 (new name for Lacépède's *La Roussatre*): No locality.

1835. *Pentonyx Capensis* Duméril & Bibron, Erpét. Gén., **2**, p. 390, pl.

[11] Some authorities would relegate this race and its forms to the synonymy of *subrufa*. It is separated here in order to stimulate inquiry as to whether or not 75 per cent of the northern population have their pectoral shields separated on the median line of the plastron — the sole character allegedly separating the two races. *P. g. disjuncta*, if indeed it actually came from Madagascar, may be a throwback for these do occur, though very rarely, within the range of the typical *s. subrufa*.

xix, figs. 2-2b: restricted by Mertens to Cape of Good Hope, South Africa.

1849. *Pentonix americana* Cornalia, Vert. Synop. Mus. Mediolan, p. 13: "in flumine propre Novaeboracum," i.e. New York (error).

1855. *Pelomedusa Mozambica* "Peters M.S.S. 1848" Gray (*Nomen nudum*), Cat. Shield Rept. Brit. Mus., p. 53: Mozambique.

1856. *Pelomedusa mossambicensis* "Peters" Lichtenstein & v. Martens, (*nomen nudum*) Nomencl. Rept., p. 2: Mozambique.

1863. *Pelomedusa nigra* Gray, Ann. Mag. Nat. Hist., (3) **12**, p. 99: Natal, South Africa.

1910. ?*Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, Hist. Phys. Nat. Pol. Madagascar, **17**, p. 56: Madagascar.[12]

1935. *Pelomedusa galeata orangensis* Hewitt, Rec. Albany Mus., **4**, p. 332, pl. xxxi, fig. 3; pl. xxxii, figs. 3-4: Kimberley, Cape Province, South Africa.

1935. *Pelomedusa galeata devilliersi* Hewitt, Rec. Albany Mus., **4**, p. 337, pl. xxxi, figs. 2 and 4: Besondermeid, Steinkopf, Cape Province, South Africa.

1935. *Pelomedusa galeata damarensis* Hewitt, Rec. Albany Mus., **4**, p. 338, pl. xxxiii, figs. 1-4: Quickborn Farm, near Okahandja, Southwest Africa.

1937. *Pelomedusa subrufa wettsteini* Mertens, Zool. Anz., **117**, p. 141, figs. 1 and 4: Majunga, western Madagascar.

Range. Dry savanna of southern Sudan east to British Somaliland, south through Uganda;[12] Kenya Colony and Tanganyika Territory to Natal, west through Cape Province to Southwest Africa, north and northeast to Belgian Congo.

Genus **PELUSIOS** Wagler

1830. *Pelusios* Wagler, Nat. Syst. Amphib., p. 137. Type by monotypy: *Emys castanea* Schweigger = *Testudo subnigra* Lacépède.

1863. *Tanoa* Gray, Proc. Zool. Soc. London, p. 193. Type by monotypy: *Sternothaerus sinuatus* A. Smith.

1863. *Notoa* Gray, Proc. Zool. Soc. London, p. 195. Type by monotypy: *Sternothaerus subniger* Gray = *Testudo subnigra* Lacépède.

Pelusios subniger (Lacépède)[13] Black Terrapin

1788. *Testudo subnigra* Lacépède, Hist. Nat. Quad. ovip. Serpens, 1. Synopsis Methodica (also p. 175, pl. xiii as *La Noiratre*): No locality.

[12] But see note under *Pelomedusa s. olivacea* (Schweigger).

[13] From this synonymy I have removed *Sternotherus niger* Duméril & Bibron, together with its synonym *S. oxyrhinus* Boulenger, as they represent a valid West African species.

1798. *Testudo nigricans* Donndorff, Zool. Beytrage Linn. Natur. **3**, p. 34 (new name for *La Noiratre* Lacépède): No locality.

1814. *Emys castanea* Schweigger, Prodromi Mon. Chelon., p. 45 (new name for *subnigra* Daudin in Paris Museum): No locality.

1825. *Sternothaerus Leachianus* Bell, Zool. Journ., **2**, p. 306: No locality.

1844. *Sternotherus Derbianus* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 37: Gambia (restricted).

1851. *Sternotherus nigrescens* Bianconi (lapsus for *nigricans* used in the text), Spec. Zool. Mosamb., Rept., pl. vii.

1886. *Pelomedusa Jouberti* Rochebrune, Vertebrata nov. Africae occident., Part 3, p. 10: Noki, Congo River, Angola; Landana, Cabinda; and Mellacorée River, French Guinea.

1906. *Sternothaerus nigricans seychellensis* Siebenrock, in Voeltzkow, Reise in Ostafrika, **2**, p. 38: Gloriosa Island.

1927. *Pelusios nigricans rhodesianus* Hewitt, Rec. Albany Mus., **4**, p. 375, figs. 1a, 1c; pl. xxvi, figs. 2-3: Mpika District, Northern Rhodesia.

1931. *Pelusios nigricans castanoides* Hewitt, Ann. Natal Mus., **6**, p. 463, pl. xxxvi, figs. 1-2: Richard's Bay, Zululand.

1932. *Pelusios bechuanicus* FitzSimons, Ann. Transvaal, Mus., **15**, p. 37: Thamalakane River at Maun, Bechuanaland Protectorate.

Range. Uganda; Kenya Colony; Tanganyika Territory and islands of the Indian Ocean (Pemba; Zanzibar; Seychelles; Madagascar; Mauritius). In east, south to Zululand, Natal, northwest to Angola; Senegal and Cape Verde Islands, east to Uganda.

Pelusios sinuatus (Smith) Serrated Terrapin

1838. *Sternotherus sinuatus* A. Smith, Illus. Zool. S. Africa, Rept., pl. i: In rivers to the north of 25° S., South Africa.

1848. *Sternotherus dentatus* Peters, Arch. Anat. Phys., p. 494: No locality.

1895. *Sternothaerus bottegi* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2) **15**, p. 9, pls. i-ii: Bardera, Somalia.

1927. *Pelusios sinuatus zuluensis* Hewitt, Rec. Albany Mus., **4**, p. 360, fig. 1d, pl. xx, figs. 1-3: near Umsinene River, Zululand.

1933. *Pelusios sinuatus leptus* Hewitt, Occ. Papers Rhodesian Mus., p. 45, pl. ix, figs. 1-2: Isoka, Northern Rhodesia.

Range. Somalia, south through Kenya Colony and Tanganyika Territory to Natal, northwest to the eastern Belgian Congo.[14]

[14] Unknown from Uganda and Lake Victoria, for early records from the Sesse Islands and Bukoba were based on misidentified *subniger*.

Subclass ARCHOSAURIA

Order CROCODYLIA[15]

Family CROCODYLIDAE

Genus **CROCODYLUS** Laurenti[16]

1763. *Crocodylus* Gronovius, Zoophyl. Gronov., fasc. 1, p. 10. Rendered unavailable by the Internat. Comm. on Zool. Nomen.[17]

1768. *Crocodylus* Laurenti, Syn. Rept., p. 53. Type by subsequent designation of Stejneger & Barbour:1917: *C. niloticus* Laurenti = *Lacerta crocodilus* Linnaeus (part).

1789. *Crocodilus* Bonnaterre (part), Tabl. Encycl. Méthod. Règnes Nat., Erpét., p. 32. Emendation for *Crocodylus* Laurenti.

1820. *Champse* Merrem, Vers. Syst. Amphib., p. 36. Type by subsequent designation: *Crocodilus biscutatus* Cuvier = *C. acutus* Cuvier.

1844. *Mecistops* Gray (part), Cat. Tort. Croc. Amphis. Brit. Mus. Type by subsequent designation *Crocodilus cataphractus* Cuvier.

1844. *Oopholis* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 58. Type by subsequent designation of Deraniyagala: *Crocodilus porosus* Schneider

1844. *Palinia* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 60. Type by monotypy: *Crocodilus rhombifer* Cuvier.

1844. *Motinia*[18] Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 60. Type by monotypy: *Crocodilus americanus* Schneider = *C. acutus* Cuvier.

1862. *Bombifrons* Gray, Ann. Mag. Nat. Hist., (3) **10**, p. 269. Type by subsequent designation: *Crocodilus bombifrons* Gray = *C. palustris* Lesson.

1862. *Temsacus* Gray, Ann. Mag. Nat. Hist., (3) **10**, p. 272. Type by monotypy: *Crocodilus intermedius* Graves.

1874. *Philas* Gray, Proc. Zool. Soc. London, p. 188. Type by monotypy: *Crocodilus johnsoni* Krefft = *C. johnstoni* Krefft.

Crocodylus cataphractus Cuvier Long-nosed Crocodile

1801. ?*Crocodilus niger* Latreille, in Buffon, Hist. Nat. Rept. (ed. Déterville), **1**, p. 210: Senegal River, Senegal.

[15] Generally accepted by herpetologists in preference to LORICATA which has been applied to pangolins and other groups.

[16] The skull from "Afrika ?" named *Champse brevirostris* (or *Crocodilus krevirostris* in the caption to figs.) Werner, 1933, Zool. Anz., **102**, p. 100, figs. 1-2, has been identified as the Aslatic *Crocodylus palustris* Lesson by Wermuth, 1953, Mitt. Zool. Mus. Berlin, **29**, p. 472.

[17] See Opinions and Declarations, 1926, in Smithsonian Misc. Coll., **73**, pp. 27-33.

[18] A misprint, corrected to *Molinia* by Gray, 1862, Ann. Mag. Nat. Hist., (3) **10**, p. 272.

1824. *Crocodilus cataphractus* Cuvier, Rech. Ossem. foss. Quad., ed. 2, **5**, p. 58, pl. v, figs. 1-2: No locality.

1835. *Crocodilus leptorhynchus* Bennett, Proc. Zool. Soc. London, p. 129: Fernando Po.

1844. *Mecistops Bennettii* Gray (new name for *C. leptorhynchus* Bennett), Cat. Tort. Croc. Amphis. Brit. Mus., p. 57.

Range. Near Ujiji, Lake Tanganyika, Tanganyika Territory, west to Angola, northwest to Senegal.

Crocodylus niloticus Laurenti Nile Crocodile

1768. *Crocodylus niloticus* Laurenti (part), Syn. Rept., p. 53: Egypt (restricted).

1768. *Crocodylus africanus* Laurenti (part; with part lizard, so unidentifiable), Syn. Rept., p. 54: No locality.

1807. *Crocodilus vulgaris* Cuvier, Ann. Mus. Hist. Nat. (Paris), **10**, p. 40, pls. i-iii: Egypt.

1807. *Crocodilus suchus* Geoffroy Saint-Hilaire, Ann. Mus. Hist. Nat. (Paris), **10**, p. 84, pl. iii: Nile and Niger Rivers.

1824. *Crocodilus Chamses* Bory de Saint-Vincent, Dict. Class. Hist. Nat., **5**, p. 105: Nile, Egypt.

1826. *Crocodilus multiscutatus* Rüppell, in Cretzschmar, Iris (Frankfurt am Main), **25**, p. 99: Soucot, Nile, "Nubia" i.e. Kordofan, Sudan.

1827. *Crocodilus marginatus* Geoffroy Saint-Hilaire, Crocodiles, in Descr. Egypte, p. 260: Nile River near Thebes, Egypt.

1827. *Crocodilus lacunosus* Geoffroy Saint-Hilaire, Crocodiles, in Descr. Egypte, p. 261: (mummy) Egypt.

1827. *Crocodilus complanatus* Geoffroy Saint-Hilaire, Crocodiles, in Descr. Egypte, p. 263: (mummy) Egypt.

1831. *Alligator cowiei* A. Smith, S. African Quart. Journ., (5) p. 15: "Rivers beyond Currichane," i.e. Rustenburg, western Transvaal.

1831. *Crocodilus Octophractus* Gray, in Griffith, Animal Kingdom, **9**, Synopsis, p. 22: Soucot, Nile River, Kordofan, Sudan.

1857. *Crocodilus Binuensis* Baikie, Proc. Zool. Soc. London, p. 48: Benue and Niger Rivers, Nigeria.

1872. *Crocodilus madagascariensis* Grandidier, Ann. Sci. Nat. Zool. (Paris), **15**, art. 20, p. 6: Madagascar.

1872. *Crocodilus robustus* Grandidier & Vaillant, C. R. Acad. Sci. (Paris), **75**, p. 150: (fossil) Amboulintsatre, Madagascar.

1886. *Crocodilus hexaphractos* Rüppell (*nomen nudum*), in Schmidt, Ber. Senckenberg. Naturf. Ges., for 1885, p. 131.

1948. *Crocodylus niloticus worthingtoni* Deraniyagala, Spolia Zeylanica (Colombo), **25**, 2, p. 30: Lake Baringo, Kenya Colony.

1948. *Crocodylus niloticus pauciscutatus* Deraniyagala, Spolia Zeylanica (Colombo), **25**, 2, p. 31: Lake Rudolf, Kenya Colony.

Range. Uganda; Kenya Colony; Tanganyika Territory: also most lakes and rivers of Africa from about 20° N., south to Tugela River, Natal. Zanzibar[19] and other islands (Seychelles; Comoros; Madagascar) of the Indian Ocean; also present in the Zerka River, Jordan.

Genus **OSTEOLAEMUS** Cope

1861. *Ostcolaemus* Cope, Proc. Acad. Nat. Sci. Philadelphia for 1860, p. 549. Type by monotypy: *Osteolaemus tetraspis* Cope.

1862. *Halcrosia* Gray, Ann. Mag. Nat. Hist., (3) **10**, p. 273. Type by monotypy: *Crocodilus frontatus* Murray.

1919. *Ostcoblepharon* K. P. Schmidt, Bull. Amer. Mus. Nat. Hist., **39**, p. 420. Type by original designation: *O. osborni* Schmidt.

Osteolaemus tetraspis osborni (Schmidt)
Eastern Broad-nosed Crocodile

1919. *Osteoblepharon osborni* K. P. Schmidt, Bull. Amer. Mus. Nat. Hist., **33**, p. 421, figs. 2-5, pl. xiii, fig. 1: Niapu, Belgian Congo.

Range. Western Uganda and eastern Belgian Congo.[20]

Subclass SYNAPTOSAURIA

Order SQUAMATA

Suborder SAURIA[21]

Family EUBLEPHARIDAE[22]

Genus **HOLODACTYLUS** Boettger

1893. *Holodactylus* Boettger, Zool. Anz., **16**, p. 113. Type by monotypy: *H. africanus* Boettger.

Holodactylus africanus Boettger

1893. *Holodactylus africanus* Boettger, Zool. Anz., **16**, p. 114: "Abdallah," i.e. Abdulla, north of Webi Shebeli, Ethiopia.

[19] As an accidental visitor: now mounted in the Peace Memorial Museum, Zanzibar.

[20] Fortunately the only Uganda specimen was photographed prior to its escape. The typical form (*O. t. tetraspis* Cope) ranges from the western Belgian Congo and Angola, northwest to Senegal.

[21] LACERTILIA of Owen (1842), Boulenger (1885) and others.

[22] Geckos with true eyelids. This family, long merged with the GEKKONIDAE, was revived by Underwood (1954, Proc. Zool. Soc. London, **124**, p. 476).

1915. *Holodactylus aculeatus* Calabresi, Monit. Zool. Ital. (Firenze) **26**, p. 238, fig. 2: Somalia.

Range. Ethiopia and British Somaliland, south through Somalia to Kenya Colony.

Family GEKKONIDAE

Genus **STENODACTYLUS** Fitzinger

1826. *Stenodactylus* Fitzinger, Neue Class. Rept., pp. 13, 47. Type by tautonomy: *S. elegans* Fitzinger, new name for *Ascalabotes stenodactylus* (*sic*) Lichtenstein.

1842. *Tolarenta* Gray, Zool. Misc., p. 58. Type by monotypy: *T. wilkinsonii* Gray = *Ascalabotes sthenodactylus* Lichtenstein.

1874. *Ceramodactylus* Blanford, Ann. Mag. Nat. Hist., (4) **13**, p. 454. Type by monotypy: *C. doriae* Blanford.

Stenodactylus sthenodactylus sthenodactylus (Lichtenstein)

1823. *Ascalabotes sthenodactylus* Lichtenstein, Verz. Doubl. Mus. Zool. Berlin, p. 102: Egypt and Nubia, i.e. Sudan.

1823. *Agame ponctué* Geoffroy Saint-Hilaire, Rept., in Descr. Égypte, **1**, p. 129, pl. v, fig. 2: Egypt.

1826. *Stenodactylus elegans* Fitzinger (new name for *Ascalabotes stenodactylus* (*sic*) Lichtenstein), Neue Class. Rept., p. 47.

1827. *Trapelus Savignyi* Audouin, Hist. Nat. Rept., in Descr. Égypte, **1**, p. 167, and Suppl. Rept., pl. i, figs. 3^1—3^3: Egypt.

1829. *Stenodactylus guttatus* Cuvier, Règne Animal, ed. 2, **2**, p. 58, pl. iv, fig. 2: Egypt.

1842. *Tolarenta Wilkinsonii* Gray, Zool. Misc., p. 59: Egypt.

1943. *Stenodactylus stenodactylus zavattari* Scortecci, Miss. Biol. Sagan-Omo, Zool., **1**, pp. 268, 294: Elolo, Olo River, Lake Rudolf, Ethiopia.[23]

Range. Syria; Arabia; Egypt, west to Tunisia, south to Lake Rudolf, Kenya Colony.

[23] Scortecci (*loc. cit.*), while stating that his two specimens from Lake Rudolf agree in most respects with *S. s. sthenodactylus*, claims that they may be differentiated by two characters. His North African material had 9-10 upper labials, his Ethiopian geckos 13-14. The counts for twelve North African *S. s. sthenodactylus* examined for my 1947 revision of the GEKKONIDAE, ranged from 9-15 (p. 46).

A new character used by Scortecci is the number of granules around midbody. In his North African specimens these were 85 and 96 respectively; in his Ethiopian geckos 105 and 106. Owing to the small and irregular size and disposition of these granules it is difficult to obtain the same number in two counts. but our material gives the following:

♂	(M.C.Z. 31395) Port Sudan, Sudan	91 or 95
♀	(M.C.Z. 51659) Ein el Weibeh, Israel	98 or 100
♀	(M.C.Z. 21909) Sfax, Tunisia	102 or 105
♂	(M.C.Z. 5234) "Dalmatia"	119 (A.L. and B.S.)

Genus **CNEMASPIS** Strauch

1887. *Cnemaspis* Strauch, Mém. Acad. Imp. Sci. St.-Pétersbourg, (7) **35**, No. 2, p. 4. Type by monotypy: *C. boulengeri* Strauch.

1921. *Paragonatodes* Noble, Amer. Mus. Novit., No. 4, p. 14. Type by original designation: *Gonatodes dickersoni* Schmidt = *G. quattuorseriatus* Sternfeld.

Cnemaspis quattuorseriatas (Sternfeld)

1912. *Gonatodes quattuorseriatus* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 202, pl. vi, fig. 1: Rugege Forest and Kisenyi, Lake Kivu, Belgian Ruanda-Urundi; Uvira, Lake Tanganyika, Belgian Congo.

1919. *Gonatodes dickersoni* Schmidt, Bull. Amer. Mus. Nat. Hist., **39**, p. 436, fig. 6: Medje, Ituri District, Belgian Congo.

1950. *Cnemaspis bohmanni* Müller & Uthmöller, Zool. Anz., **145**, p. 118: Mto-wa-Mbu, 990 metres, at foot of Great Rift Valley about 2 km. north of Lake Manyara, Tanganyika Territory.

Range. Kenya Colony, south to central Tanganyika Territory, west through Uganda and Belgian Ruanda-Urundi to the Belgian Congo.

Cnemaspis africana elgonensis Loveridge

Elgon Forest-Gecko

1936. *Cnemaspis africanus elgonensis* Loveridge, Proc. Zool. Soc. London, p. 820: Above Sipi, western slopes of Mount Elgon, Uganda.

Range. Western Kenya Colony to Mount Ruwenzori, western Uganda.

Cnemaspis africana africana (Werner)

Usambara Forest-Gecko

1895. *Gymnodactylus africanus* Werner, Verh. Zool. Bot. Ges. Wien, **45**, p. 190, pl. v, fig. 5: Usambara Mountains, Tanganyika Territory.

Range. Central Kenya Colony, south to eastern Tanganyika Territory.

The locality of this last gecko is no doubt erroneous, it having been received from a dealer in February, 1884.

Genus **HEMIDACTYLUS** Oken

1817. *Hemidactyles* Cuvier, Règne Animal, **2**, p. 47. Only included species the "G. Tuberculeux de Daud.," i.e. *Gecko tuberculosus* Daudin = *Gecko mabouia* Moreau de Jonnés.

1817. "*Hemidact*" von Oken, Isis, col. 1183. Assumed abbreviation for *Hemidactylus*.[24] No species mentioned.

1825. *Hemidactylus* Gray, Ann. Philos., **26**, p. 119, "Old Continent. *H. tuberculosus* Gray. *Gecko*. Daud."

1827. *Hemidactylus* Gray, Philos. Mag., (n.s.) **2**, p. 55. The only species included is "*Gecko tuberculosus* Daud."

1842. *Boltalia* Gray, Zool. Misc., p. 58. Type by monotypy: *B. sublaevis* Gray.

1843. *Hoplopodion* Fitzinger, Syst. Rept., pp. 19, 103. Type by original designation: *Hemidactylus coctaei* Duméril & Bibron.

1843. *Microdactylus* Fitzinger, Syst. Rept., pp. 19, 104. Type by original designation: *Hemidactylus peruvianus* Wiegmann.

1843. *Onychopus* Fitzinger, Syst. Rept., pp. 19,104. Type by original designation: *Hemidactylus garnotii* Duméril & Bibron.

1843. *Tachybates* Fitzinger, Syst. Rept., pp. 19, 105. Type by original designation: *Gecko mabouia* Moreau de Jonnés.

1843. *Pnoëpus* Fitzinger, Syst. Rept., pp. 19, 106. Type by original designation: *Hemidactylus javanicus* Cuvier = *H. frenatus* Duméril & Bibron.

1845. *Velernesia* Gray, Cat. Lizards Brit. Mus., p. 156. Type by monotypy: *V. richardsonii* Gray.

1845. *Doryura* Gray, Cat. Lizards Brit. Mus., p. 156. Type by subsequent designation: *D. bowringii* Gray.

1845. *Leiurus* Gray (not of Hemprich & Ehrenberg), Cat. Lizards Brit. Mus., p. 157. Type by monotypy: *L. ornatus* Gray = *Hemidactylus f. fasciatus* Gray.

1845. *Nubilia* Gray, Cat. Lizards Brit. Mus., p. 273. Type by monotypy: *N. argentii* Gray = *Hemidactylus depressus* Gray.

[24] Oken, though only contrasting his own classification with that of Cuvier, frequently latinized the latter's vernacular names. In this instance he lists "Gecko . . . Thecadactylus Hemidact. Platydact." The assumption that he intended "ylus" endings, rather than "yles," is open to question.

In his description of *Gecko tuberculosus*, Daudin (1802) states that it has narrow scales beneath the tail: this agrees with *mabouia* Moreau de Jonnés and excludes the confusion of some authors with *Gecko gecko* of Siam, for the latter has transverse rows of small quadrangular scales beneath its tall. Furthermore, under "*G. mabuia* Nob." Cuvier remarks in the 1820 edition of Règne Animal, that this gecko is called Mabouia des murailles in the islands, being found in all the warmer parts of America. A footnote adds that this is the "Mabouia des murailles" recently monographed by Moreau de Jonnés. I am not sure why Sherborn regarded *Hemidactylus* Gray, 1825, as a *nomen nudum* unless it is on account of the erroneous "Old Continent." For Gray furnishes a brief description, though possibly not diagnostic. The first use of the name *Hemidactylus* approved by Sherborn is that of Gray, 1827.

1846. *Hoplopodium* Agassiz, Nomen. Zool., Index Univers., p. 185. Emendation for *Hoplopodion* Fitzinger.

1861. *Eurhous* Fitzinger, Sitzb. Akad. Wiss. Wien, **42**, p. 400. Type by monotypy: *Hemidactylus leschenaultii* Duméril & Bibron.

1862. *Liurus* Cope (not of Ehrenberg:1828), in Slack, Handbook Mus. Acad. Nat. Sci. Philadelphia, p. 32. New name for *Leiurus* Gray (preoccupied).

1869. *Teratolepis* Günther, Proc. Zool. Soc. London, p. 504. Type by monotypy: *Hormonota fasciata* Blyth.

1894. *Bunocnemis* Günther, Proc. Zool. Soc. London, p. 85. Type by monotypy: *B. modestus* Günther.

1934. *Lophopholis* Smith & Deraniyagala, Ceylon Journ. Sci., (B) **18**, p. 235. Type by original designation: *Teratolepis scabriceps* Annandale.

1940. *Aliurus* Dunn & Dunn, Copeia, p. 71. New name for *Liurus* Cope (preoccupied).

Hemidactylus albopunctatus Loveridge

1942. *Teratolepis taylori* Parker (not *Hemidactylus taylori* Parker: 1932), Bull. Mus. Comp. Zool., **91**, p. 33: Haud at 8° 15′N., 46° 20′E., 2100 feet, British Somaliland.

1947. *Hemidactylus albopunctatus* Loveridge (new name for *Teratolepis taylori* Parker:preoccupied), Bull. Mus. Comp. Zool., **98**, p. 107.

Range. British Somaliland, south to northern Kenya Colony.

Hemidactylus isolepis Boulenger

1895. *Hemidactylus isolepis* Boulenger, Proc. Zool. Soc. London, p. 531, pl. xxix, fig. 1: Turfa Tug, south of Harar, Ethiopia.

Range. Ethiopia and British Somaliland, south through Somalia to Kenya Colony.

Hemidactylus modestus (Günther)

1894. *Bunocnemis modestus* Günther, Proc. Zool. Soc. London, p. 95, pl. viii: Ngatana, Tana River, Kenya Colony.

Range. Kenya Colony (known only from the type locality).

Hemidactylus tropidolepis Mocquard

1888. *Hemidactylus tropidolepis* Mocquard, Mém. Cent. Soc. Philom. Paris, p. 133: Somaliland.

Range. British Somaliland, south to the Tana River, Kenya Colony.

Hemidactylus squamulatus squamulatus Tornier[25]

[25] Though at one time I regarded this and the following form as races of *tropidolepis* Mocquard, since collecting the latter it seems advisable to treat the much larger *squamulatus* as distinct.

1896. *Hemidactylus squamulatus* Tornier, Die Kriechthiere Deutsch-Ost-Afrikas, p. 10: Kakoma, Ugunda, Tanganyika Territory.

1896. *Hemidactylus bocagei* Tornier (not of Boulenger), Die Kriechthiere Deutsch-Ost-Afrikas, p. 12: Dalalani, Lake Natron, Tanganyika Territory.

1897. *Hemidactylus werneri* Tornier (new name for *H. bocagei* Tornier: preoccupied), Arch. Naturg., **63**, Abt. 1, p. 63.

1902. *Hemidactylus Tornieri* Mocquard (new name for *H. bocagei* Tornier: preoccupied), Bull. Mus. Hist Nat. (Paris), **8**, p. 407.

1923. *Hemidactylus Alluaudi* Angel, Bull. Mus. Hist. Nat. (Paris), **29**, p. 490: Bura, Teita, Kenya Colony.

Range. Northeastern Kenya Colony, south to central Tanganyika Territory.

Hemidactylus squamulatus barbouri Loveridge

1942. *Hemidactylus tropidolepis barbouri* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 320, fig. —: Changamwe, Kenya Colony.

Range. Coastal Kenya Colony from Malindi, south to Tanga, Tanganyika Territory.

Hemidactylus frenatus Duméril & Bibron

1836. *Hemidactylus frenatus* "Schlegel" Duméril & Bibron, Erpét. Gén., **3**, p. 366: Java (restricted); South Africa, etc.

1843. *Hemidactylus* (*Phoepus*) *javanicus* "Cuvier" Fitzinger, Syst. Rept., p. 106: Java (restricted).

1843. *Hemidactylus* (*Phoepus*) *Bojeri* Fitzinger, Syst. Rept., p. 106: Cape of Good Hope; Madagascar; Mauritius.

1845. *Hemidactylus vittatus* Gray, Cat. Lizards Brit. Mus., p. 155: Borneo.

1854. ?*Hemidactylus punctatus* Jerdon, Journ. Asiatic Soc. Bengal, **22**, p. 467 (type lost): Tellicherry, Malabar, India.

1860. *Hemidactylus inornatus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 492: Riu Kiu Islands.

1860. *Hemidactylus pumilus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 502: Hongkong.

1864. *Gecko chaus* Tytler, Journ. Asiatic Soc. Bengal, (2) **33**, p. 547: Rangoon, Burma (restricted).

1864. *Gecko caracal* Tytler, Journ. Asiatic Soc. Bengal, (2) **33**, p. 547: Rangoon, Burma.

1868. *Hemidactylus longiceps* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 320: Manila, Philippine Islands.

1868. *Hemidactylus hexaspis* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 320: Madagascar.

1915. *Hemidactylus fragilis* Calabresi, Monit. Zool. Ital. (Firenze), **26**, p. 236, fig. 1: Bur Meldac, Somalia.

Range. Somaliland; Lamu Island; Seychelles; Mauritius; Madagascar; St. Helena and other islands of the Indian and Pacific Oceans; Ceylon; southern India; Malay Peninsula; Indo-China; China; Korea (This wide distribution may be attributed to human agency).

Hemidactylus puccionii Calabresi

1927. *Hemidactylus puccionii* Calabresi, Atti. Soc. Ital. Sci. Nat. (Milano), **66**, pp. 23, 39, pl. i, figs. 3-3b: Obbia to Durgale, Somalia.

1936. *Hemidactylus parkeri* Loveridge, Proc. Biol. Soc. Washington, **49**, p. 59: Zanzibar Island (? introduced).

Range. Somalia and Zanzibar Island (? introduced).

Hemidactylus citernii Boulenger

1912. *Hemidactylus citernii* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (3) **5**, p. 329: Rahanuin country, Somalia.

Range. British Somaliland, south through Somalia to Kenya Colony (? introduced. Erroneously reported from Tanganyika and Zanzibar).

Hemidactylus brookii angulatus Hallowell

1852. *Hemidactylus angulatus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 63, fig. —: "West coast of Africa," i.e. Gabon, French Congo.

1868. *Hemidactylus guineensis* Peters, Monatsb. Akad. Wiss. Berlin, p. 640: "Ada Foah, Guinea," i.e. Adafer, Mauritania.

1870. *Hemidactylus affinis* Steindachner, Sitzb. Akad. Wiss. Wien, **62**, Abt. 1, p. 328: Dagana and Goree, Senegal.

1885. *Hemidactylus stellatus* Boulenger, Cat. Lizards Brit. Mus., **1**, p. 130, pl. xii, fig. 1: Gambia and West Africa.

1893. *Hemidactylus Bayonii* Bocage, Jorn. Sci. Lisboa, (2) **3**, p. 116: Dondo, Cuanza River, Angola.

1897. *Hemidactylus brookii* var. *Togoensis* Werner, Verh. Zool. Bot. Ges. Wien, **47**, p. 397: Atakpamé, Togo.

Range. Sudan and Uganda, south to Tanganyika Territory, west through Belgian Congo to Angola and French Congo, northwest to Senegal and the Cape Verde Islands. (Its distribution is due in part to human agency. Another race occurs in the West Indies and South America; two in Asia.)

Hemidactylus turcicus macropholis Boulenger

1896. *Hemidactylus macropholis* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2) **17**, p. 7, pl. i, figs. 2-2c: Dolo, Somalia.

Range. Ethiopia and British Somaliland, south through Somalia to Kenya Colony. (Another race occurs in Arabia, as does the typical form whose wide distribution in four continents is in part due to human agency.)

Hemidactylus ruspolii Boulenger

1896. *Hemidactylus ruspolii* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2) **17**, p. 6, pl. i, figs. 1-1c: Bardera; Dolo; Lugh; Magala and Umberto Island, Somalia.

1907. *Hemidactylus erlangeri* Steindachner, Ann. Akad. Wiss. Wien, **44**, p. 355: Ethiopia.

Range. Ethiopia and British Somaliland, south to northern Kenya Colony.

Hemidactylus tanganicus Loveridge

1929. *Hemidactylus tanganicus* Loveridge, U. S. Nat. Mus. Bull., 151, p. 42, pl. i: Dutumi, near Kisaki, Tanganyika Territory.

Range. Tanganyika Territory (known only from the large holotype).

Hemidactylus mabouia (Jonnés) Common House-Gecko

1802. *Gecko tuberculosus* Daudin, Hist. Nat. Rept., **4**, p. 158, footnote: No locality.

1818. *Gecko Mabouia* Moreau de Jonnés, Bull. Soc. Philom. Paris, p. 138: Antilles and adjacent mainland.

1825. *Gecko aculeatus* Spix, Animalia Nova Species Novae Lacerta., p. 16, pl. xviii, fig. 3: Rio de Janeiro, Brazil.

1825. *Gecko cruciger* Spix, Animalia Nova Species Novae Lacerta., p. 16: Bahia, Brazil.

1825. *Gekko incanescens* Wied, Beitr. Naturg. Brasilien, **1**, p. 101: Brazil.

1825. *Gekko armatus* Wied, Beitr. Naturg. Brasilien, **1**, p. 104: Brazil.

1854. ?*Hemidactylus platycephalus* Peters, Monatsb. Akad. Wiss. Berlin, p. 615: Coast north of Mozambique; Johanna Island, Comoro Islands.

1867. *Hemidactylus Sakalava* Grandidier, Revue Mag. Zool., (2) **19**, p. 233: Tulear, Madagascar.

1879. *Hemidactylus frenatus* var. *calabaricus* Boettger, Ber. Offenbach. Ver. Naturk., 17-18, p. 1: Old Calabar, Nigeria.

1893. *Hemidactylus benguellensis* Bocage, Jorn. Sci. Lisboa, (2) **3**, p. 115: Cahata, Benguela, Angola.

1932. *Hemidactylus tasmani* Hewitt, Ann. Natal Mus., **7**, p. 120: Driefontein, near Gwelo, Southern Rhodesia.

Range. Possibly Eritrea and Ethiopia; certainly Somalia south through Kenya Colony; Tanganyika Territory; Pemba, Zanzibar and Mafia Islands to Zululand; northwest through Transvaal and Beehuanaland to Angola; north and northwest to Liberia. (In West Africa, however, the distribution is spotty, presumably due to introduction at ports.) West Indies. Mexico. South America. Madagascar.

Hemidactylus mercatorius Gray Coconut-Palm Gecko

1842. *Hemidactylus mercatorius* Gray, Zool. Misc., p. 58: Madagascar.

1909. *Hemidactylus gardineri* Boulenger, Trans. Linn. Soc. London, (2) **12**, p. 296, pl. xi, fig. 4: Farquhar Island, Seychelle Islands.

1928. *Hemidactylus persimilis* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 140, pl. iv, figs. 1, 3: Dar es Salaam, Tanganyika Territory.

1936. *Hemidactylus mandanus* Loveridge, Proc. Biol. Soc. Washington, **49**, p. 60: Kitau, Manda Island, Kenya Colony.

Range. Coastal Kenya Colony and Tanganyika Territory; including Pemba Island (and almost certainly Zanzibar and Mafia Islands), the Seychelle and Aldabra Islands, Madagascar and Mauritius; south to Mozambique, inland to Nyasaland.

Genus **LYGODACTYLUS** Gray

1864. *Lygodactylus* Gray, Proc. Zool. Soc. London, p. 59. Type by monotypy: *L. strigatus* Gray = *Hemidactylus capensis* A. Smith.

1880. *Scalabotes* Peters, Monatsb. Akad. Wiss. Berlin, p. 795. Type by monotypy: *S. thomensis* Peters.

1883. *Microscalabotes* Boulenger, Ann. Mag. Nat. Hist., (5) **11**, p. 174. Type by monotypy: *M. cowani* Boulenger.

Lygodactylus somalicus Loveridge

1935. *Lygodactylus somalicus somalicus* Loveridge, Proc. Biol. Soc. Washington, **48**, p. 196: Bar Madobe, Nogal Valley, British Somaliland.

1935. *Lygodactylus somalicus annectens* Loveridge, Proc. Biol. Soc. Washington, **48**, p. 197: Buran District, British Somaliland.

Range. British Somaliland, south through Somalia to Kenya Colony.

Lygodactylus scheffleri Sternfeld

1912. *Lygodactylus fischeri scheffleri*, Sternfeld, Wiss. Ergebn. Deut.

Zentral-Afrika-Exped. 1907-1908, **4**, p. 206: Kibwezi, Kenya Colony.

Range. Kenya Colony.

Lygodactylus conradti Matschie

1892. *Lygodactylus conradti* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 109: Derema, Usambara Mountains, Tanganyika Territory.

Range. Kenya Colony and Tanganyika Territory.

Lygodactylus angolensis Bocage

1896. *Lygodactylus angolensis* Bocage, Jorn. Sci. Lisboa, (2) **4**, p. 110: Hanha, Benguela, Angola.

1926. *Lygodactylus stevensoni* Hewitt, Ann. Natal Mus., **5**, p. 445, pl. xxv, figs. 3-4: Khami Ruins, Bulawayo, Southern Rhodesia.

1933. *Lygodactylus laurae* Schmidt, Ann. Carnegie Mus., **22**, p. 4: Chitau, Bihe District, Angola.

Range. Tanganyika Territory, south to Southern Rhodesia, west through Bechuanaland to Angola and the Belgian Congo.

Lygodactylus capensis (Smith) Cape Dwarf-Gecko

1849. *Hemidactylus capensis* A. Smith, Illus. Zool. S. Africa, Rept., pl. lxxv, fig. 3: Kaffirland and districts north of Cape Province.

1864. *Lygodactylus strigatus* Gray, Proc. Zool. Soc. London, p. 59: "Southeastern Africa," i.e. Zambezi region.

1932. *Lygodactylus bradfieldi* Hewitt, February, Ann. Natal Mus., **7**, p. 126, pl. vi, fig. 10: Quickborn Farm, near Okahandja, Southwest Africa.

1932. *Lygodactylus capensis ngamiensis* FitzSimons, October, Ann. Transvaal Mus., **15**, p. 35: Mabeleapudi, Ngamiland, Bechuanaland Protectorate.

Range. Kenya Colony and Tanganyika Territory, south to Natal, west through northern Cape Province to Southwest Africa and Angola.

Lygodactylus grotei grotei Sternfeld

1911. *Lygodactylus Grotei* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 245: Mikindani, etc., Tanganyika Territory.

1920. *Lygodactylus capensis mossambica* Loveridge, Proc. Zool. Soc. London, p. 135: Lumbo, Mozambique.

Range. Tanganyika Territory and Mafia Island, south to Mozambique.

Lygodactylus grotei pakenhami Loveridge

Pemba Island Dwarf-Gecko

1941. *Lygodactylus grotei pakenhami* Loveridge, Proc. Biol. Soc. Washington, **54**, p. 176: Wete, Pemba Island.

Range. Pemba Island.

Lygodactylus angularis angularis Günther

1893. *Lygodactylus angularis* Günther, Proc. Zool. Soc. London, 1892, p. 555, pl. xxxiii, figs. 1-3: Shire Highlands, Nyasaland.

Range. Tanganyika Territory and Nyasaland, west to Northern Rhodesia.

Lygodactylus picturatus gutturalis (Bocage)

1873. *Hemidactylus gutturalis* Bocage, Jorn. Sci. Lisboa, **4**, p. 211: Bissau, Portuguese Guinea.

Range. Uganda and Tanganyika Territory (Ujiji only), west to French Congo. Portuguese Guinea.

Lygodactylus picturatus keniensis Parker

1936. *Lygodactylus picturatus keniensis* Parker, Ann. Mag. Nat. Hist., (10) **18**, p. 602: Lodwar, Lake Rudolf, Kenya Colony.

Range. Kenya Colony (north of the Uaso Nyiro).

Lygodactylus picturatus ukerewensis Loveridge

1935. *Lygodactylus picturatus ukerewensis* Loveridge, Proc. Biol. Soc. Washington, **48**, p. 199: Ukerewe Island, Lake Victoria, Tanganyika Territory.

Range. Kenya Colony and Tanganyika Territory (in vicinity of Lake Victoria).

Lygodactylus picturatus mombasicus Loveridge

1935. *Lygodactylus picturatus mombasicus* Loveridge, Proc. Biol. Soc. Washington, **48**, p. 198: Kilindini, Mombasa Island, Kenya Colony.

Range. Coastal Kenya Colony (meets with typical form at both Mombasa and Tanga), south to Tanga, Tanganyika Territory.

Lygodactylus picturatus picturatus (Peters)

Yellow-headed Dwarf-Gecko

1868. *Hemidactylus variegatus* Peters (not of Duméril & Bibron:1836), Monatsb. Akad. Wiss. Berlin, p. 449: "Zanzibar Coast," i.e. Tanganyika Territory.

1870. *Hemidactylus picturatus* Peters (new name for *variegatus* Peters: preoccupied), Monatsb. Akad. Wiss. Berlin, p. 115.

1896. *Lygodactylus picturatus* vars. *griseus, septemlineatus* and *quin-*

quelineatus Tornier (*nomina nuda*), Die Kriechthiere Deutsch-Ost-Afrikas, p. 15: No types or type localities designated.

1928. *Lygodactylus manni* Loveridge, Proc. U. S. Nat. Mus., **72**, Art. 24, p. 1, pl. i: Saranda, Ugogo, Tanganyika Territory.

Range. (Somalia ? or) Kenya Colony (coastal belt from Mombasa) south to Tanganyika Territory and Mozambique (chiefly coast, rivers and railways); Zanzibar and Mafia Islands. Northern Rhodesia and neighboring parts of the Belgian Congo (its present distribution has been complicated by transportation as eggs or adults through human agency).

Lygodactylus picturatus williamsi Loveridge

Turquoise-Blue Dwarf-Gecko

1952. *Lygodactylus picturatus williamsi*[26] Loveridge, Journ. E. Africa Nat. Hist. Soc., vol. "xx," p. "446," = **21**, p. 39: Kimboza Forest, 1000 feet, Eastern Province, Tanganyika Territory.

Range. Tanganyika Territory (known only from the holotype).

Genus **PHYLLODACTYLUS** Gray[27]

1828. *Phyllodactylus* Gray, Spicil. Zool., p. 3. Type by monotypy: *P. pulcher* Gray.

1843. *Euleptes* Fitzinger, Syst. Rept., pp. 18, 95. Type by original designation: *Phyllodactylus europaeus* Gené.

1843. *Discodactylus* Fitzinger, Syst. Rept., pp. 18, 95. Type by original designation: *Phyllodactylus tuberculosus* Wiegmann.

1845. *Gerrhopygus* Gray, Cat. Lizards Brit. Mus., p. 150. Type by tautonomy: *Diplodactylus gerrhopygus* Wiegmann.

1879. *Paroedura* Günther, Ann. Mag. Nat. Hist., (5) **3**, p. 218. Type by monotypy: *P. sanctijohannis* Günther.

Phyllodactylus wolterstorffi (Tornier)[28]

1900. *Diplodactylus wolterstorffi* Tornier, Zool. Jahrb., Syst., **13**, p. 584, fig. A: Tanga, Tanganyika Territory.

[26] Altered by the then editor to *Williamsi* in some printings, to *villiamsi* in others; both volume number and pagination were in error, so corrected in a subsequent issue by the new editor.

[27] Here used in the new sense proposed by Garth Underwood (1954, Proc. Zool. Soc. London, **124**, p. 472) involving the transfer to *Phyllodactylus* of those species with a *Gekko*-type pupil formerly referred to *Diplodactylus*, a genus now restricted to Australia.

[28] Through the kindness of Dr. Heinz Wermuth, I recently had the opportunity of examining the type and a paratype (now M.C.Z. 54700). They reveal some minor defects in Tornier's description, but though there is little to differentiate them from *P. inexpectatus* (Stejneger)of the Seychelles, direct comparison with a specimen of the latter (M.C.Z. 49198) shows that the two are distinct.

Range. Tanganyika Territory (known only from the four types).

Genus **EBENAVIA** Boettger

1878. *Ebenavia* Boettger, Abhand. Senckenberg. Naturf. Ges., **11**, p. 276. Type by monotypy: *E. inunguis* Boettger.

Ebenavia sp.[29]

Range. Pemba Island.

Genus **PHELSUMA** Gray

1825. *Phelsuma* Gray, Ann. Philos., (2) **10**, p. 199. Type by monotypy: "*P. crepidianus*," i.e. *Gecko cepedianus* Merrem.

1830. *Anoplopus* Wagler, Nat. Syst. Amphib., p. 142. Type by designation of Fitzinger:1843: *Gecko cepedianus* Merrem.

Phelsuma dubia dubia (Boettger)

1881. *Pachydactylus dubius* Boettger, Zool. Anz., **4**, p. 46: Madagascar.

Range. Coastal Tanganyika Territory; Zanzibar Island; Comoro Islands; northwest Madagascar.

Phelsuma madagascariensis parkeri Loveridge

1941. *Phelsuma madagascariensis parkeri* Loveridge, Proc. Biol. Soc. Washington, **54**, p. 175: Kinowe, Pemba Island.

Range. Pemba Island.

Genus **HOMOPHOLIS** Boulenger

1885. *Homopholis* Boulenger, Cat. Lizards Brit. Mus., **1**, p. 191. Type by monotypy: *Gecko walbergi* (*sic*) A. Smith.

[29] Admission of this genus to the East African list rests solely on some geckos newly hatched from eggs, measuring 5 x 6 mm., found at Chokocho and Kinangaju, Pemba Island, by R. H. Pakenham (1947, Ann. Mag. Nat. Hist., (11) **14**, p. 135). The assignment to *Ebenavia* is unquestionably correct; it was made by H. W. Parker. At my request he very kindly re-examined them *under very high magnification* supplying me with a sketch and the substance of the following:

Scales of head multicarinate, uniform, their size corresponding to the larger body granules; the latter have some indications of a keel, all the dorsal granules appearing to be subimbricate with a surface sculpturing of minute papillae; among them are irregular rows of large rounded tubercles; no enlarged chin shields; no claws. Color above, pale straw, with or without a few, very faint, longitudinal lines that converge upon the base of tail; the dorsal color sharply demarcated from that on the sides of head, neck and flanks, this is dark sepia passing gradually into the light sepia of the undersurface; tail above displays some paired spots anteriorly, while posteriorly it is banded with darker and lighter. This is, of course, hatchling coloration and probably differs from that of the adult. Capture of some adults on Pemba is necessary to settle the point as to whether the species is distinct, or whether *inunguis* Boettger has been introduced from Nosy Be, Madagascar, and become established on Pemba.

1890. *Platypholis* Boulenger, Proc. Zool. Soc. London, p. 80, pl. vii, fig. 2. Type by monotypy: *P. fasciata* Boulenger.

Homopholis fasciata fasciata (Boulenger)

1890. *Platypholis fasciata* Boulenger, Proc. Zool. Soc. London, pp. 77, 81, pl. viii, fig. 2: Mombasa, Kenya Colony.

Range. Northern Kenya Colony, south to Tanganyika Territory.

Genus **PACHYDACTYLUS** Wiegmann

1834. *Pachydactylus* Wiegmann, Herp. Mexicana, p. 19. Type by monotypy: *P. bergii* Wiegmann = *Lacerta geitje* Sparrman.

1843. *Colobopus* Fitzinger, Syst. Rept., p. 19. Type by original designation: *Anoplopus inunguis* Wagler = *Gecko inunguis* Cuvier, 1817 = *Lacerta geitje* Sparrman, 1778.

1845. *Cantinia* Gray, Cat. Lizards Brit. Mus., pp. 167, 168. Type by monotypy: *Pachydactylus elegans* Gray = *Tarentola capensis* A. Smith.

1864. *Homodactylus* Gray (not Fitzinger:1843), Proc. Zool. Soc. London, p. 59. Type by monotypy: *H. turneri* Gray.

1894. *Elasmodactylus* Boulenger, Proc. Zool. Soc. London, p. 724. Type by monotypy: *E. tuberculosus* Boulenger.

Pachydactylus bibronii turneri (Gray)

1864. *Homodactylus turneri* Gray, Proc. Zool. Soc. London, p. 59, pl. ix, fig. 2: Tete, Mozambique.

1910. *Pachydactylus bibronii* var. *stellatus* Werner, Denks. Med.-Nat. Ges. Jena, **16**, p. 309: Great Namaqualand, Southwest Africa.

Range. Belgian Ruanda-Urundi and Tanganyika Territory, south to Mozambique, west through Nyasaland; the Rhodesias; Transvaal; Bechuanaland and Orange Free State to Little Namaqualand and adjacent Cape Province, north through Southwest Africa to southern Angola.

Pachydactylus tetensis Loveridge

1952. *Pachydactylus tetensis* Loveridge, Bull. Mus. Comp. Zool., **110**, p. 175, pl. v, fig. 3: Mwanza Rocks, Kasumbadedza, near Tete, Mozambique.

Range. Near Liwale, Tanganyika Territory, south to Mozambique (on south bank of the Zambezi).

Pachydactylus tuberculosus (Boulenger)

1894. *Elasmodactylus tuberculosus* Boulenger, Proc. Zool. Soc. London,

pp. 723, 727, pl. xlvii, fig. 2: Lower Congo.

1896. *Pachydactylus boulengeri* Tornier, Die Kriechthiere Deutsch-Ost-Afrikas, p. 26, pl. ii, fig. 1: Tabora and Kakoma, Tanganyika Territory.

1913. *Elasmodactylus triedrus* Boulenger, Revue Zool. Afr., **3**, p. 104, figs. —: Kikondja, Katanga, Belgian Congo.

Range. Tanga, Tanganyika Territory, southwest to Nyamkolo, Northern Rhodesia; west to Lower Congo River; Belgian Congo.

Family AGAMIDAE

Genus **AGAMA** Daudin[30]

1802. *Agama* Daudin (part), Hist. Nat. Rept., **3**, pp. 333, 356. Type by subsequent designation: *A. colonorum* Daudin (part) = *Lacerta agama* Linnaeus.

1817. *Trapelus* Cuvier, Règne Animal, **2**, p. 35. Type by monotypy: *Agame variabile* Geoffroy = *Agama mutabilis* Merrem.

1826. *Tapaya* Fitzinger, Neue Class. Rept., pp. 17, 49. Type by subsequent designation: *Agama orbicularis* Cuvier = *Lacerta hispida* Linnaeus.

1833. *Cyclosaurus* Wagler, Isis von Oken, col. 894. Type by original designation: *Agama orbicularis* Daudin = *Lacerta hispida* Linnaeus.

1843. *Phrynopsis* Fitzinger, Syst. Rept., pp. 17, 79. Type by original designation: *Agama atra* Daudin.

1843. *Podorrhoa* Fitzinger, Syst. Rept., pp. 18, 80. Type by original designation: *Agama colonorum* Daudin = *Lacerta agama* Linnaeus.

1843. *Pseudotrapelus* Fitzinger, Syst. Rept., pp. 18, 81. Type by original designation: *Agama sinaita* Heyden.

1843. *Planodes* Fitzinger, Syst. Rept., pp. 18, 81. Type by original designation: *Agama agilis* Olivier.

1843. *Trapeloidis* Fitzinger, Syst. Rept., pp. 18, 81. Type by original designation: *Lacerta sanguinolenta* Pallas.

1843. *Psammorrhoa* Fitzinger, Syst. Rept., pp. 18, 81. Type by original designation: *Agama aculcata* Merrem.

1843. *Eremioplanis* Fitzinger, Syst. Rept., pp. 18, 82. Type by original

[30] Elimination of *Stellio* Laurenti (part), 1768, Syn. Rept., p. 56, was achieved by subsequent designation of its type as *S. saxatilis* Laurenti by Stejneger, in M. A. Smith, 1933, Journ. Bombay Nat. Hist. Soc. for 1932, **35**, p. 619. *S. saxatilis*, being based on Seba, 1735, Locup. Rerum Nat. Thesaurus, **2**, pl. lxxix, fig. 4, is declared unrecognizable. The genus *Stellio* has been used in other senses by Schneider (1792); Latreille (1802); Wagler (1830) and others.

Intentionally omitted from the synonymy are obvious misspellings such as *Trapetus* Oken (1817); *Tapelus* Gray (1825); *Cyoclosaurus* Wagler (1833).

designation: *Trapelus aegyptius* Cuvier = *Agama mutabilis* Merrem.

1843. *Acanthocercus* Fitzinger, Syst. Rept., pp. 18, 84. Type by original designation: *Stellio cyanogaster* Rüppell.

1845. *Laudakia* Gray, Cat. Lizards Brit. Mus., p. 254. Type by monotypy: *Agama tuberculata* Gray.

1845. *Isodactylus* Gray, Cat. Lizards Brit. Mus., p. 259. Type by monotypy: *Agama sinaita* Heyden.

1854. *Plocederma* Blyth, Journ. Asiatic Soc. Bengal, **23**, p. 738. Type by monotypy: *Laudakia* (*Plocederma*) *melanura* Blyth.

1856. *Brachysaura* Blyth, Journ. Asiatic Soc. Bengal, **25**, p. 448. Type by monotypy: *B. ornata* Blyth = *Agama minor* Hardwicke & Gray.

1860. *Barycephalus* Günther, Proc. Zool. Soc. London, p. 150. Type by monotypy: *B. sykesii* Günther = *Agama tuberculata* Gray.

1895. *Xenagama* Boulenger, Proc. Zool. Soc. London, p. 534. Type by original designation: *Uromastix batilliferus* Vaillant.

Agama ruppelli occidentalis Parker[31]
Western Arboreal-Agama

1932. *Agama rueppelli occidentalis* Parker, Journ. Linn. Soc. London, Zool., **38**, p. 225: near mouth of Kaliokwell River, Lake Rudolf, Kenya Colony.

Range. Southern Ethiopia to northern Kenya Colony.

Agama ruppelli septentrionalis Parker
Southern Arboreal-Agama

1932. *Agama rueppelli septentrionalis* Parker, Journ. Linn. Soc. London, Zool., **38**, p. 225: Mount Nyero (as Njiro); Madago's village; Voi and Mbunyi, Kenya Colony.

Range. Central and southern Kenya Colony.

Agama hispida armata Peters[32] Peters' Spiny Agama

1854. *Agama armata* Peters, Monatsb. Akad. Wiss. Berlin, p. 616: Rios de Sena; Tete, Mozambique.

Range. Tanganyika Territory, south through Mozambique; Nyasaland and the Rhodesias to Natal.

Agama mossambica mossambica Peters Mozambique Agama

1854. *Agama mossambica* Peters, Monatsb. Akad. Wiss. Berlin, p. 616: Coast of Mozambique.

[31] *A. vaillanti* Boulenger is a synonym of *A. r. ruppelli* Vaillant of Ethiopia and the Somalilands. Kenya records of *vaillanti* should be referred to one or other of Parker's races.

[32] Early East African records of *hispida* or *hispida distanti* Boulenger should be referred to this race, the other two races being South African.

1874. *Agama cariniventris* Peters, Monatsb. Akad. Wiss. Berlin, p. 159: Zanzibar Coast; i.e. Tanganyika Territory.

Range. Tanganyika Territory, south through northern Mozambique and Nyasaland to Northern Rhodesia.[33]

Agama mossambica montana Barbour & Loveridge[34] Montane Rock-Agama

1928. *Agama mossambica montana* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 147: below Bagilo, Uluguru Mountains, Tanganyika Territory.

Range. Usambara and Uluguru Mountains, Tanganyika Territory.

Agama agama agama (Linnaeus) Common Rock-Agama

1758. *Lacerta agama* Linnaeus (part), Syst. Nat., ed. 10, **1**, p. 207: "America" (error).

1802. *Agama colonorum* Daudin, Hist. Nat. Rept., **3**, p. 356: "Amérique meridionale," etc. (error).

1831. *Agama Occipitalis* Gray, in Griffith, Animal Kingdom, **9**, Synopsis, p. 56: Africa.

1877. *Agama colonorum* var. *congica* Peters, Monatsb. Akad. Wiss. Berlin, p. 612: Chinchoxo, Cabinda.

1877. *Agama picticauda* Peters (? part[35]) Monatsb. Akad. Wiss. Berlin, p. 612: "Ada Foah," i.e. ? Adafer, Mauretania, French West Africa; Accra, Gold Coast; also Cameroon.

Range. Southern Sudan and Uganda, west to Nigeria, south to Angola.

Agama agama lionotus Boulenger Kenya Rock-Agama

1896. *Agama lionotus* Boulenger, Proc. Zool. Soc. London, p. 214, pl. viii: southeast of Lake Rudolf, Kenya Colony.

Range. Eastern Uganda (Suk), southeast to Voi, Kenya Colony.

Agama agama usambarae Barbour & Loveridge Usambara Rock-Agama

1928. *Agama colonorum usambarae* Barbour & Loveridge, Mem. Mus.

[33] The two young agamas from Athi Plains, Kenya Colony, referred to *mossambica* by Mocquard (1902, Bull. Mus. Hist. Nat. (Paris), **8**, p. 405) are possibly *A. a. lionotus*, a species that occurs there (M.C.Z. 44260-1).

[34] I have long thought that *montana* is a full species but, pending a thorough revision of the entire genus, consider it is best left as described. *A. m. mossambica* occurs on the lower slopes of the Uluguru range.

[35] While Cameroon specimens are unquestionably *A. a. agama*, our Gold Coast material seems nearer to the western race *A. a. africana* Hallowell. The question cannot be settled until a series from Ada Foah has been studied, being an area where the races meet.

Comp. Zool., **50**, p. 150, pl. ii, fig. 1: Soni, Usambara Mountains, Tanganyika Territory.

Range. Usambara Mountains, Tanganyika Territory.

Agama agama elgonis Lönnberg Elgon Rock-Agama

1922. *Agama elgonis* Lönnberg, Arkiv. Zool., **14**, No. 12, p. 2: Mount Elgon, Kenya Colony.

1932. *Agama agama turuensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 376: Unyanganyi, Turu, Tanganyika Territory.

Range. Uganda and Kenya slopes of Mount Elgon, south to Usandawi in central Tanganyika Territory.

Agama agama dodomae Loveridge Dodoma Rock-Agama

1923. *Agama lionotus* var. *dodomae* Loveridge, Proc. Zool. Soc. London, p. 944: Dodoma, Ugogo, Tanganyika Territory.

Range. Central to southwestern Tanganyika Territory.

Agama agama ufipae Loveridge Ufipa Rock-Agama

1932. *Agama agama ufipae* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 377: near Kipili, Ufipa, Tanganyika Territory.

Range. Western Tanganyika Territory (Lake Tanganyika).

Agama planiceps mwanzae Loveridge Mwanza Rock-Agama

1923. *Agama lionotus* var. *mwanzae* Loveridge, Proc. Zool. Soc. London, p. 945: Shanwa, Mwanza, Tanganyika Territory.

Range. Northwestern Tanganyika Territory.

Agama planiceps caudospina Meek Elmenteita Rock-Agama

1910. *Agama caudospina* Meek, Field Mus. Nat. Hist., Zool. Series, **7**, p. 407: Lake Elmenteita, Kenya Colony.

1935. *Agama agama kaimosae* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 10: near Kaimosi, Kakamega, Kenya Colony.

Range. Kenya Colony.

Agama annectens Blanford Eritrean Rock-Agama

1870. *Agama annectens* Blanford, Zool. Abyssinia, p. 446, fig. —: "Sooroo" i.e. Suru Pass, Eritrea.

Range. Eritrea, Ethiopia and the Somalilands, south to northern Kenya Colony.

Agama cyanogaster (Rüppell) Black-necked Arboreal-Agama

1835. *Stellio cyanogaster* Rüppell, Neue Wirbelth. Fauna Abyssinica, Amphib., p. 10, pl. v: Massaua, Eritrea.

1849. *Agama atricollis* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 14: Natal, South Africa.

1851. *Stellio Capensis* A. Duméril, Cat. Méthod. Coll. Rept. Mus. Paris, p. 106: "Cape of Good Hope," i.e. South Africa.

1866. *Stellio nigricollis* Bocage, Jorn. Sci. Lisboa, **1**, p. 43: Duque de Braganca, Huila Plateau, Mossamedes, Angola.

1894. *Agama gregorii* Günther, Proc. Zool. Soc. London, p. 86: Mkonumbi, near Lamu, Kenya Colony.

Range. Eritrea, south through Ethiopia; Uganda; Kenya Colony and Tanganyika Territory (apparently absent from the coastal islands of Pemba, Zanzibar and Mafia!) to Natal, northwest through Bechuanaland to Ovamboland, Southwest Africa; Angola and Belgian Congo.

Family CHAMAELEONIDAE[36]

Genus **CHAMAELEO** Laurenti

1763. *Chamacleon* Gronovius,[37] Zoophyl. Gronov. . . ., p. 12.

1768. *Chamaelco* Laurenti, Syn. Rept., p. 45. Type by subsequent designation: *C. parisiensium* Laurenti = *Lacerta chamaeleon* Linnaeus.

1839. *Diceros* Swainson, Nat. Hist. Fishes, Amph. Rept., **2**, pp. 347, 369. Type by monotypy: *D. bifurcatus* Swainson.

1839. *Trioceros* Swainson, Nat. Hist. Fishes, Amph. Rept., **2**, pp. 347, 369. Type by monotypy: *T. grayii* Swainson.

1843. *Triceras* Fitzinger, Syst. Rept., pp. 15, 42. Type by original designation: *Chamaeleo oweni* Gray.

1843. *Furcifer* Fitzinger, Syst. Rept., pp. 15, 42. Type by original designation: *Chamaeleon bifidus* Brongniart.

1843. *Bradypodion* Fitzinger, Syst. Rept., pp. 15, 43. Type by original designation: *Chamaeleon pumilus* Latreille = *Lacerta pumila* Gmelin.

1846. *Bradypodium* Agassiz, Nomen. Zool., Index Univers., p. 52. Emendation for *Bradypodion* Fitzinger.

1865. *Apola* Gray, Proc. Zool. Soc. London for 1864, pp. 467, 473. Type by monotypy: *Chamaeleo lateralis* Gray.

[36] CHAMAELEONTIDAE, derived from CHAMAELEONTES Fitzinger (1843: 41) is rejected. This family was for long referred to a separate suborder (RHIPTOGLOSSA) on account of the peculiar projectile tongue possessed by all its members. In recent years, however, this separation has been considered of less significance than the obvious relationship to the AGAMIDAE, from which stock chameleons appear to have been derived.

[37] A work specifically rejected from taxonomic purposes in rule 89 of the Internat. Comm. Zool. Nomencl. — cf. 1926, Proc. Biol. Soc. Washington, **39**, p. 103. Omitted are the numerous variations such as: *Chameleo* (Bonnaterre: 1789); *Cameleo* (Bosc:1803); *Camaeleo* (Duméril:1806); *Chameleon* (Fleming: 1822); *Chaelio* (A. Smith:1831); *Chamaeleon* (Fitzinger:1843); *Camaelcon* (Duméril & Bibron:1863); some intentional emendations, others due to carelessness.

1865. *Pterosaurus* Gray, Proc. Zool. Soc. London for 1864, pp. 467, 473. Type by monotypy: *Chamaeleo cristatus* Stutchbury.

1865. *Microsaura*[38] Gray, Proc. Zool. Soc. London for 1864, pp. 467, 473. Type by monotypy: *M. melanocephala* Gray.

1865. *Phumanola* Gray, Proc. Zool. Soc. London for 1864, pp. 467, 474. Type by monotypy: *Chamaeleo namaquensis* A. Smith.

1865. *Lophosaura* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 474. Type by restriction: *Lacerta pumila* Gmelin.

1865. *Calumma* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 476. Type by monotypy: *Chamaeleo cucullatus* Gray.

1865. *Crassonota* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 477. Type by monotypy: *Chamaeleo nasutus* Duméril & Bibron.

1865. *Ensirostris* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 478. Type by monotypy: *E. melleri* Gray.

1865. *Sauroceras* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 478. Type by monotypy: *Chamaeleo rhinoceratus* Gray.

1865. *Dicranosaura* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 478. Type by restriction: *Chamaeleo bifurcus* Gray = *C. bifidus* Brongniart.

1865. *Cyneosaura* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 479. Type by monotypy: *Chamaeleo pardalis* Cuvier.

1865. *Calyptrosaura* Gray, Proc. Zool. Soc. London for 1864, p. 468. Type by present designation: *Chamaeleo calyptratus* A. Duméril.

1865. *Erizia* Gray, Proc. Zool. Soc. London for 1864, p. 471. Type by present designation: *Chamaeleo senegalensis* Daudin.

1865. *Dilepis* Gray, Proc. Zool. Soc. London for 1864, p. 472. Type by tautonomy: *Chamaeleo dilepis* Leach.

1865. *Archaius* Gray, Proc. Zool. Soc. London for 1864, p. 475. Type by present designation: *Chamaeleo tigris* Kuhl.

1956. *Bicuspis* Loveridge, Breviora (Cambridge, Mass.), No. 59, p. 2. Type by original designation: *Rhampholeon marshalli* Boulenger.[39]

Chamaeleo senegalensis senegalensis Daudin

Senegal Chameleon

1802. *Chamaeleo senegalensis* Daudin, Hist. Nat. Rept., **4**, p. 203: Region watered by the Senegal and Niger Rivers; Gambia and Guinea.

[38] *Microsaura*. Under this name FitzSimons (1943: Transvaal Mus. Mem., 1, p. 158), following Power (1932: Proc. Zool. Soc. London, p. 209) who, however, used *Lophosaura*, would grant generic status to a group of South African chameleons of which the best known is *pumilus*. If this course is followed, then *Bradypodion* (*Bradypodium* of Gray) Fitzinger takes precedence over *Microsaura*, for Fitzinger definitely states: "Typus. *Cham. pumilus* Latr." Tentatively I prefer to regard the group as subgeneric, but those who differ should remove these three genera from the synonymy of *Chamaeleo*.

[39] A prehensile-tailed species, but with the bicuspid claws of a *Rhampholeon*; occupying an intermediate position between the two genera, hence *Bicuspis*.

1863. *Chamaeleo laevigatus* Gray, Proc. Zool. Soc. London, p. 95: Five hundred miles south of Khartoum, Sudan.

1864. *Chamaeleon senegalensis* var. *?leiocephalus* Gray, Proc. Zool. Soc. London, p. 471: Type in British Museum. No locality.

1887. *Chamaeleon sphaeropholis* Reichenow, Zool. Anz., **10**, p. 370: Kagera, west of Lake Victoria, Tanganyika Territory.

1951. *Chamaeleon senegalensis* v. *Tibaticnsis* Monard, Mem. Inst. Franc. Afrique Noire (Sci. Nat.), No. 1, p. 141: Tibati, French Cameroon.

Range. Sudan, east to Eritrea, south through Ethiopia to Uganda; Kenya Colony and western Tanganyika Territory. Recorded from Angola and the Belgian Congo, northwest to Sierra Leone (M.C.Z. material) and Senegal.

Chamaeleo senegalensis anchietae Bocage[40]

Angola Chameleon

1872. *Chamaeleo Anchietae* Bocage, Jorn. Sci. Lisboa, **4**, p. 72, fig. —: Huila, Mossamedes, Angola.

1950. *Chamaeleo* (*Apola*) *vinckei* Laurent, Revue Zool. Bot. Afr., **43**, p. 349: Swampy grassland sources of the Lofoi River at 1750 metres, near Kundelungu Plateau Research Station, Katanga, Belgian Congo.

1952. *?Chamaeleo anchietae mertensi* Laurent, Revue Zool. Bot. Afr. **46**, p. 18: Muneshele, 1400 metres, Fizi Territory, Kivu, Belgian Ruanda-Urundi.

1952. *?Chamaeleo anchietae marunguensis* Laurent, Revue Zool. Bot. Afr., **46**, p. 19: Kipiri, 2000 metres, Marungu Plateau, Baudouinville Territory, Tanganyika Province, Belgian Congo.

Range. Highlands of southern Tanganyika Territory, west through highlands of eastern and southern Belgian Congo to Angola.

Chamaeleo gracilis gracilis Hallowell Graceful Chameleon

1842. *Chamaeleo gracilis* Hallowell, Journ. Acad. Nat. Sci. Philadelphia, **8**, p. 324, pl. xviii: Liberia.

1856. *Chamaeleo granulosus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 147: West Africa.

1856. *Chamaeleo Burchelli* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 147: Fernando Po.

[40] I have not seen *mertensi* and *marungensis* which were based on scanty material (a ♂, ♀ and juvenile of the former, two ♀ ♀ of the latter), but I have compared a ♀ paratype of *vinckei* (M.C.Z. 53262) with a Tanganyika ♀ (M.C.Z. 31186) and failed to find differences that would justify its description.

1885. *Chamaeleo* (*Chamaeleo*) *Simoni* Boettger, Ber. Offenbach Ver. Naturk., p. 175, footnote: Mountains of Ashanti, Gold Coast.

Range. French Somaliland, south through Uganda and Kenya Colony to northern Tanganyika Territory (Longido and Meru Mountains), west through the Belgian Congo (? and Angola) where it meets with the race *etiennei* Schmidt (characterized by spurless ♂♂) found around Banana; northwest (though not definitely reported from the French Congo; Nigeria and Dahomey) to Senegal.

Chamaeleo dilepis roperi Boulenger[41]

Spurless Flap-necked Chameleon

1890. *Chamaeleon roperi* Boulenger, Proc. Zool. Soc. London, p. 85, pl. viii, fig. 4: Kilifi, north of Mombasa, Kenya Colony.

Range. Eastern Kenya Colony (Meru to Tana River) and northeast Tanganyika Territory (around Kilimanjaro Mtn. only).

Chamaeleo dilepis quilensis Bocage[42] (doubtfully distinct)

1866. *Chamaeleo dilepis* var. *Quilensis* Bocage, Jorn. Sci. Lisboa, **1**, p. 59: Rio Quilo, north of Cabinda, Cabinda.

1887. *Chamaeleon parvilobus* Boulenger, Cat. Lizards Brit. Mus., **3**, p. 449, pl. xxxix, fig. 5: Natal; French Congo; Cameroon.

Range. (in part, being based solely on material in the M.C.Z. from) Kenya Colony; Tanganyika Territory; Southern Rhodesia; Transvaal; Zululand; Natal; Southwest Africa; Angola; Belgian Congo; French Congo; French Cameroon.

Chamaeleo dilepis dilepis Leach[43]

Spurred Flap-necked Chameleon

[41] Distinguished only by the ♂♂ being spurless like the ♀♀; being identifiable only on the basis of adult ♂♂, records require careful screening and the range working out with considerable care.

[42] As this form, whose ♂♂ are usually spurred, is separable from *d. dilepis* solely on the small size of its occipital flaps, subadult *d. dilepis* are apt to be reported as *d. quilensis* with resulting confusion. M.C.Z. material reveals *both* forms as present in five widely scattered countries. While a good series from a given locality is likely to be readily assignable to one form or the other, solitary specimens are often intermediate in the degree of flap development. That we are dealing with two sibling species seems improbable. FitzSimons (1943, Transvaal Mus. Mem. No. 1, pp. 155-156) resolves that dilemma by according *quilensis* varietal rank in order to indicate that it is something less than a subspecies. His volume should be consulted for records of *both* forms south of the Zambezi.

[43] Other apparently valid races occurring on the periphery of British East Africa, and approached by individuals within the territories, are:

Chamaeleo dilepis petersii Gray, 1864, of Mozambique.

Chamaeleo dilepis isabellinus Günther, 1893 (1892), from the Shire Highlands of Nyasaland.

Chamaeleo dilepis ruspolii Boettger, 1893, from Ogaden, Somalia.

1819. *Chamaeleo dilepis* Leach, in Bowdich, Miss. Ashantee, App., p. 493: French Congo.

1820. *Chamaeleo bilobus* Kuhl, Beitr. Zool. Anat., **1**, p. 104: French Congo.

1820. *Chamaeleo planiceps* Merrem, Vers. Syst. Amph., p. 162: Africa.

1864. *Chamaeleon petersii* var. *kirkii* Gray, Proc. Zool. Soc. London, p. 470: East Africa.

1866. *Chamaeleo Capellii* Bocage, Jorn. Sci. Lisboa, **1**, pp. 42, 59: Benguela, Angola.

1903. *Chamaeleo angusticoronatus* Barbour, Proc. Biol. Soc. Washington, **16**, p. 61: Zanzibar Island.

Range. (in part, being based solely on material in the M.C.Z. from) Kenya Colony; Tanganyika Territory; Pemba and Zanzibar Islands; Nyasaland; Northern Rhodesia; Southern Rhodesia; Cabinda; Belgian Congo.

Chamaeleo bitaeniatus bitaeniatus Fischer[44]

Side-striped Chameleon

1884. *Chamaeleo bitaeniatus* Fischer, Jahrb. Hamburg, Wiss. Anst., **1**, p. 23, pl. ii, figs. 7a-b: Lake Naivasha, Kenya Colony.

1887. *Chamaeleo bivittatus* (*lapsus: nomen nudum*) F. Müller, Verh. Naturf. Ges. Basel, **8**, p. 294: Witu, Kenya Colony.

Range. Ethiopia and Somalia, south through Uganda and Kenya Colony to northern and western Tanganyika Territory.

Chamaeleo bitaeniatus ellioti Günther

Montane Side-striped Chameleon

1895. *Chamaeleon Ellioti* Günther, Ann. Mag. Nat. Hist., (6) **15**, p. 524, pl. xxi, fig. A: Bugoye, east foot of Ruwenzori Mountains, Uganda.

1912. *Chamaeleon bitaeniatus graueri* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 380, pl. xv, figs. 19-21, pl. xvii, fig. 33: Bugoie and Rugege Forests above 2000 metres, Belgian Ruanda-Urundi.

1912. *Chamaeleon bitaeniatus tornieri* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 383, pl. xvii, fig. 35: Lendu Plateau, Ituri District, Belgian Congo.

[44] Owing to sexual or individual variation, members of the *bitaeniatus* group are exceptionally difficult to place. Most large series are likely to contain one or more individuals strikingly different from the rest, and such outstanding specimens are apt to receive names. In addition to those listed, or tentatively synonymized, here, two others have recently been described from neighbouring territories. These are *C. b. kinetensis* K. P. Schmidt (1943) from Mount Kineti at 10,458 feet, Imatong Mountains, southern Sudan, which appears to be intermediate between typical *bitaeniatus* and *b. ellioti;* also *C. b. schoutedeni* Laurent (1952) from Kabumbe Valley at 2400 metres, Kabobo Mountain, Albertville Territory, Tanganyika Province, Belgian Congo.

1922. *Chamaeleon Bequaerti* Witte, Revue Zool. Bot. Afr., **10**, p. 69, pl. ii, fig. 1: Beni, Kivu District, Belgian Congo.

Range. Mountains (usually below 9000 feet) of western Uganda; Belgian Ruanda-Urundi and the adjacent Belgian Congo.

Chamaeleo bitaeniatus rudis Boulenger
Ruwenzori Side-striped Chameleon

1906. *Chamaeleon rudis* Boulenger, Ann. Mag. Nat. Hist., (7) **18**, p. 473: Ruwenzori Mountains above 10,000 feet, Uganda.

1933. *Chamaeleon Burgeoni* Witte, Revue Zool. Bot. Afr., **24**, p. 120, fig. —: Mombasa, near Lubero, Kivu District, Belgian Congo.

Range. Mountains (usually above 9000 feet) of western Uganda; Belgian Ruanda-Urundi and the adjacent Belgian Congo.

Chamaeleo bitaeniatus schubotzi Sternfeld
Kenya Side-striped Chameleon

1912. *Chamaeleon bitaeniatus schubotzi* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 381, pl. xv, fig. 24; pl. xvii, fig. 34: Mount Kenya, 14,000 feet, Kenya Colony.

Range. Alpine zones of Mounts Kinangop and Kenya, Kenya Colony; Mounts Kilimanjaro and Nguru, Tanganyika Territory.

Chamaeleo bitaeniatus höhnelii Steindachner
High-casqued Chameleon

1891. *Chamaeleon Höhnelii* Steindachner, Sitzb. Akad. Wiss. Wien., **100**, Abt. 1, p. 309, pl. i, figs. 1-1a: Laikipia, 6000 feet, Kenya Colony.

1891. *Chamaeleon leikipiensis* Steindachner, Sitzb. Akad. Wiss. Wien, **100**, Abt. 1, p. 311, pl. i, figs. 2-2a: Laikipia, 6000 feet, Kenya Colony.

1912. *Chamaeleon bitaeniatus bergeri* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, pp. 380-381, pl. xiv, fig. 16; pl. xvi, fig. 31: "Sirgoi nordl. von Ravine," i.e. Sergoit, north of Eldama Ravine Station, Kenya Colony (erroneously given as "Sirgoi südlich von Ravine," in a later paper of 1912).

Range. Highlands (usually below 9000 feet) of eastern Uganda and Kenya Colony.

Chamaeleo bitaeniatus altaeelgonis Loveridge
Alpine High-casqued Chameleon

1935. *Chamaeleon bitaeniatus altaeelgonis* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 15: Kaburomi, 10,500 feet, Mount Elgon, Uganda.

Range. Alpine zone (above 10,000 feet) of Mount Elgon, Uganda and Kenya Colony.

Chamaeleo goetzei goetzei Tornier
Tanganyika Goetze Chameleon

1899. *Chamaeleon Goetzei* Tornier, Zool. Anz., **22**, p. 413, pl. ii, fig. 3: Uhehe, Tanganyika Territory.

Range. Uzungwe; Ubena; Ukinga; Rungwe and Poroto Mountains, Tanganyika Territory.

Chamaeleo laterispinis Loveridge Spiny-sided Chameleon

1932. *Chamaeleon laterispinis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 381: Kigogo, 6000 feet, Uzungwe Mountains, Tanganyika Territory.

Range. Uzungwe Mountains, Tanganyika Territory.

Chamaeleo incornutus Loveridge Ukinga Hornless Chameleon

1932. *Chamaeleon incornutus* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 380: Madehani, 7000 feet, Ukinga Mountains, Tanganyika Territory.

Range. Ukinga; Rungwe and Poroto Mountains, Tanganyika Territory.

Chamaeleo tempeli Tornier Tubercle-nosed Chameleon

1899. *Chamaeleon Tempeli* Tornier, Zool. Anz., **22**, p. 411, pl. ii, figs. 2, 4: Uzungwe Mountains, Uhehe, Tanganyika Territory.

1900. *Chamaeleon tempeli* var. *wolffi* Tornier, Zool. Jahrb. Syst. **13**, p. 613, fig. G (captions reversed and an 'f' dropped from first *wolffi*): "Tardalla," i.e. Tandala, Ukinga Mountains, Tanganyika Territory.

Range. Uzungwe; Ubena and Ukinga Mountains, Tanganyika Territory.

Chamaeleo melleri (Gray) Giant One-horned Chameleon

1864. *Ensirostris melleri* Gray, Proc. Zool. Soc. London, p. 478, pl. xxxii, fig. 1: "Mountains in the interior of East Africa" (as collected by Dr. Meller of Zomba, restricted by Loveridge (1953) to Zomba Mountain, Nyasaland).

Range. Savanna Forests of Tanganyika Territory and Nyasaland.

Chamaeleo spinosus Matschie Rosette-nosed Chameleon

1892. *Chamaeleon spinosus* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 105: Derema, Usambara Mountains, Tanganyika Territory.

Range. Virgin Forests of Usambara Mountains, Tanganyika Territory.

Chamaeleo tenuis Matschie Single Soft-horned Chameleon

1892. *Chamaeleon tenuis* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 106; Derema, Usambara Mountains, Tanganyika Territory.

Range. Virgin Forests of Usambara Mountains, Tanganyika Territory.

Chamaeleo xenorhinus Boulenger
Single Welded-horn Chameleon

1901. *Chamaeleon xenorhinus* Boulenger, Proc. Zool. Soc. London, **2**, p. 135, pl. xii: Ruwenzori Mountains, 6000 feet, Uganda.

1929. *Chamaeleo carpenteri* Parker, Ann. Mag. Nat. Hist., (10) **3**, p. 280, fig.: Ruwenzori Mountains, 6500 feet, Uganda.

Range. Virgin Forests (above 6000 feet) of Ruwenzori Mountains, Uganda.

Chamaeleo fischeri excubitor Barbour
Kenya Hornless Chameleon

1911. *Chamaeleo tenuis excubitor* Barbour, October 31, Proc. Biol. Soc. Washington, **24**, p. 219: Meru District, Mount Kenya, Kenya Colony.

1911. *Chamaeleon affinis embuensis* Lönnberg, November 16, Svenska Vetensk.-Akad. Handl., **47**, No. 6, p. 19, pl. ii, fig. 3: Forest on eastern slopes of Mount Kenya, one day's march from Embu Boma, Kenya Colony.

Range. Virgin forests of Mount Kenya, Kenya Colony.

Chamaeleo fischeri uthmölleri Müller
Hanang Hornless Chameleon[45]

1938. *Chamaeleo uthmölleri* Müller, Zool. Anz., **122**, p. 20, figs. 1-2: Mount Hanang (Gurui or Guruwe) at 2300 feet, central Tanganyika Territory.

Range. Virgin forest of Mount Hanang, between Mkalama and Kondoa Irangi, Tanganyika Territory.

Chamaeleo fischeri tavetanus Steindachner
Kilimanjaro Two-horned Chameleon

1891. *Chamaeleon tavetanus* Steindachner, Anz. Akad. Wiss. Wien, **28**, p. 142: Taveta Forest, Kenya Colony.

1891. *Chamaeleon tavetensis* Steindachner, Sitzb. Akad. Wiss. Wien, **100**, Abt. 1, p. 312, pl. i, figs. 3-3a: Taveta Forest, Kenya Colony.

[45] Assuming that the sexing of the only known specimen is a ♂ as stated.

1891. *Chamaeleo abbotti* Stejneger, Proc. U. S. Nat. Mus., **14**, p. 353, fig. —: Mount Kilimanjaro, 4500 feet, Tanganyika Territory.

1893. *Chamaeleo taitensis* "Steind." (*sic*) Stejneger (*lapsus* for *tavetanus*), Proc. U. S. Nat. Mus., **16**, p. 724.

Range. Virgin forests of Teita Mountains, Kenya Colony, west to Kilimanjaro, Tanganyika Territory.

Chamaeleo fischeri multituberculatus Nieden

Western Usambara Two-horned Chameleon

1913. *Chamaeleon fischeri multituberculatus* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, pp. 244, 248, figs. 27-29, pl. xv, fig. 7; pl. xvi, fig. 11: "Phillipshof bei Wilhelmstal," i.e. Magamba, near Lushoto, western Usambara Mountains, Tanganyika Territory.

1913. *Chamaeleon fischeri werneri* Nieden (not of Tornier), Sitzb. Ges. Naturf. Freunde Berlin, pp. 243, 248, figs. 19-26, pl. xv, fig. 6; pl. xvi, fig. 10: Ambangula and Mlalo, western Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of western Usambara Mountains, Tanganyika Territory.

Chamaeleo fischeri fischeri Reichenow

Eastern Usambara Two-horned Chameleon

1887. *Chamaeleon Fischeri* Reichenow, Zool. Anz., **10**, p. 371: Nguru Mountains, Tanganyika Territory.

1895. *Chamaeleon matschiei* Werner, Verh. Zool. Bot. Ges. Wien, **45**, p. 192: Usambara Mountains, Tanganyika Territory.

1902. *Chamaeleon tornieri* Werner, Zool. Jahrb. Syst., **15**, p. 417, pl. xxiv: "Mozambique" (presumably in error).

1913. *Chamaeleon fischeri vosseleri* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, pp. 241, 247, figs. 11-18, pl. xv, fig. 5; pl. xvi, fig. 9: Amani; Bulwa; Nguelo in Usambara Mountains; Magrotto Mountain; Tanga, Tanganyika Territory.[46]

Range. Virgin forests of eastern Usambara Mountains, south to Nguru Mountain, Tanganyika Territory.

Chamaeleo fischeri uluguruensis Loveridge

Uluguru Two-horned Chameleon

1957. *Chamaeleo fischeri uluguruensis* Loveridge, Tanganyika Notes and Records, No. 43, p. 3: Kingokwa, Uluguru Mountains, Tanganyika Territory.

Range. Virgin forests of the Uluguru Mountains, Tanganyika Territory.

[46] Restricted as the author also lists Ukami, which is in the Uluguru Mountains; and Usaramo, i.e. Dar es Salaam region, in error.

Chamaeleo fülleborni Tornier Poroto Three-horned Chameleon

1900. *Chamaeleon fülleborni* Tornier, Zool. Jahrb. Syst., **13**, p. 614, fig. H: "Nonde-Nike," i.e. Konde and Nyika (tribes); also "Ngosi- oder Peroto-Berges um 2200 m." i..e. Ngosi or Poroto Mountains, Tanganyika Territory.

Range. Ngosi Volcano, Poroto Mountains, Ukonde, Tanganyika Territory.

Chamaeleo werneri Tornier Uzungwe Three-horned Chameleon

1899. *Chamaeleon Werneri* Tornier, Zool. Anz., **22**, p. 258, fig. 1: "Maschona-Gebiet," later corrected to Uzungwe Mountains, Uhehe, Tanganyika Territory.

1932. *Chamaeleon werneri dabagae* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 379: Dabaga, Uzungwe Mountains, Tanganyika Territory.

Range. Uluguru and Uzungwe Mountains, Tanganyika Territory.

Chamaeleo johnstoni johnstoni Boulenger
Ruwenzori Three-horned Chameleon

1901. *Chamaeleon johnstoni* Boulenger, Proc. Zool. Soc. London, **2**, p. 136, pl. xiii: Ruwenzori Mountains, 6000 feet, Uganda.

1911. *Chamaeleon graueri* Steindachner, Anz. Akad. Wiss. Wien, **48**, p. 177: Mountains northwest of Lake Tanganyika, Belgian Congo.

1912. *Chamaeleon johnstoni affinis* Sternfeld (not Rüppell), Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 262, pl. vii, fig. 3: Virgin forest behind boundary mountains on northwest shore of Lake Tanganyika, Belgian Congo.

Range. Virgin forests of Uganda; Belgian Ruanda-Urundi and the adjacent Belgian Congo.

Chamaeleo jacksonii Boulenger
Kikuyu Three-horned Chameleon

1896. *Chamaeleon Jacksonii* Boulenger, Ann. Mag. Nat. Hist., (6) **17**, p. 376: "Uganda" (error), later amended to Kikuyu, near Nairobi, Kenya Colony.

1903. *Chamaeleon jacksoni* var. *vauerescecae* Tornier, Zool. Jahrb. Syst., **19**, p. 176: Nairobi, 6000 feet, Kikuyu, Kenya Colony.

Range. Highlands of Kenya Colony and Tanganyika Territory.

Chamaeleo deremensis Matschie
Usambara Three-horned Chameleon

1892. *Chamaeleon deremensis* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 103; Derema, Usambara Mountains, Tanganyika Territory.

Range. Usambara Mountains, Tanganyika Territory.

INTRODUCED

Chamaeleo oustaleti Mocquard[47] Malagasy Giant Chameleon

1894. *Chamaeleon Oustaleti* Mocquard, C. R. Soc. Philom. Paris, No. 9, p. 3; and 1895 (1894), Bull. Soc. Philom. Paris, (8), **7**, p. 113: Betsileo and Diego Suarez, Madagascar.

Range. Madagascar; but introduced into Ngong Forest, near Nairobi, Kenya Colony.

Genus **BROOKESIA** Gray[48]

1865. *Brookesia* Gray, Proc. Zool. Soc. London for 1864, pp. 468, 476. Type by monotypy: *Chamaeleo superciliaris* Kuhl.

1874. *Rhampholeon* Günther, Proc. Zool. Soc. London, p. 443, fig. —. Type by monotypy: *Chamaeleo spectrum* Buchholz.

1942. *Evoluticauda* Angel, Mem. Acad. Malgache, No. 36, pp. 154, 178. Type by subsequent selection: *Brookesia nasus* Boulenger.[49]

Brookesia kerstenii robecchi (Boulenger)
Somalia Pigmy-Chameleon

1892. *Rhampholeon robecchii* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova for 1891, (2) **12**, p. 13, pl. i, fig. 3: "Wuorandi," i.e. Warandi, *ca.* 5° 42′ N., 47° 38′ E., Somalia.

1897. *Rhampholeon mandera* Meek, Field Mus. Nat. Hist., Zool. Series, **1**, p. 183: Mandera, British Somaliland.

Range. British Somaliland, south through Somalia to northern Kenya Colony.

Brookesia kerstenii kerstenii (Peters)
Kenya Pigmy-Chameleon

[47] On April 11, 1951, Miss V. Hardy-Mason brought to the Coryndon Memorial Museum a giant chameleon which she had captured alive at Ngong in an area undergoing deforestation.

The reptile, a male, measures 18¾ inches from end of snout to tip of tail, the latter forming 10 inches of the total. The snout does not terminate in a horn, but from the crown of the head between the eyes there rises steeply a helmet-like casque with strongly compressed median ridge. From behind this, along the spinal ridge and, to a lesser extent, along the prehensile tail, is a continuous serrated ridge formed of spinelike conical scales. A.L.

[48] Though *Rhampholeon* is inseparable from *Brookesia* on the basis of the external characters cited by Günther and Boulenger, it may well rank as a subgenus on the basis of the anatomical differences described by Parker (1942, Bull. Mus. Comp. Zool., **91**, pp. 80-81, fig. 8). In this sense all East African short-tailed chameleons are probably referable to the subgenus *Rhampholeon* whose range is Tropical Africa and Madagascar.

[49] As Angel designated no type for his genus *Evoluticauda*, I suggest the included *Brookesia nasus* be regarded as the type.

1868. *Chamaeleo Kerstenii* Peters, Monatsb. Akad. Wiss. Berlin, p. 449: "Wanga," i.e. Wange, south of Mombasa, Kenya Colony.

Range. Northern Kenya Colony, south to Tanganyika Territory.

Brookesia nchisiensis Loveridge Pitless Pigmy-Chameleon

1953. *Brookesia nchisiensis* Loveridge, Bull. Mus. Comp. Zool., **110**, p. 190, pl. iii, fig. 1: Nchisi Forest, 5000 feet, Nchisi Mountain, Nyasaland.

Range. Virgin forests of southwestern Tanganyika Territory, south to Nchisi Mountain, Nyasaland.

Brookesia brevicaudata (Matschie)
Bearded Pigmy-Chameleon

1892. *Chamaeleon* (*Brookesia*) *brevicaudatus* Matschie (19.viii.92, *fide* publishers), Sitzb. Ges. Naturf. Freunde Berlin, p. 107: Derema, Usambara Mountains, Tanganyika Territory.

1893. *Rhampholeon Boettgeri* Pfeffer, Mitt. Naturhist. Mus. Hamburg for 1892, **10**, p. 76, pl. i, figs. 6-7: Bagamoyo, Tanganyika Territory.

Range. Coastal Tanganyika Territory.

Brookesia brachyura ionidesi Loveridge
Beardless Pigmy-Chameleon

1951. *Brookesia ionidesi* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 179: Kilwa, Southern Province, Tanganyika Territory.

Range. Southeastern Tanganyika Territory.

Brookesia temporalis (Matschie) Pitted Pigmy-Chameleon

1892. *Chamaeleon* (*Brookesia*) *temporalis* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 108: Derema, Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of Usambara Mountains, Tanganyika Territory.

Brookesia spectrum boulengeri (Steindachner)
Spectral Pigmy-Chameleon

1911. *Rhampholeon boulengeri* Steindachner, Anz. Akad. Wiss. Wien, **48**, p. 178: Mountains northwest of Lake Tanganyika, Belgian Congo.

Range. Virgin forests of western Uganda and eastern Belgian Congo.

Family SCINCIDAE

Genus **MABUYA** Fitzinger

1815. *Mabuya* Rafinesque, Anal. Nat. (Palermo), p. 16. *Nomen nudum.*

1826. *Mabuya* Fitzinger (part), Neue Class. Rept., pp. 23, 52. Type by tautonomy: *M. dominicensis* Fitzinger = *Lacertus mabouya* Lacépède which Fitzinger lists as a synonym.

1826. *Spondylurus* Fitzinger, Neue Class. Rept., p. 23 only. Type by monotypy: *Scincus sloanii* Daudin.

1830. *Euprepis* Wagler (part), Nat. Syst. Amphib., pp. 132, 161. Type by subsequent designation: *Scincus agilis* Raddi = *Lacertus mabouya* Lacépède.

1839. *Herinia* Gray, Ann. Nat. Hist., **2**, p. 332. Type by monotypy: *H. capensis* Gray.

1843. *Eutropis* Fitzinger, Syst. Rept., p. 22. Type by original designation: *Euprepes sebae* Duméril & Bibron = *Scincus carinatus* Schneider (part) + *Scincus multifasciatus* Kuhl + *Euprepes macularius* Blyth.

1843. *Trachylepis* Fitzinger, Syst. Rept., p. 22. Type by original designation: *Euprepes savignyi* Duméril & Bibron = *Scincus quinquetaeniatus* Lichtenstein.

1843. *Oxytropis* Fitzinger, Syst. Rept., p. 22. Type by original designation: *Euprepes merremii* Duméril & Bibron = *Tiliqua capensis* Gray.

1845. *Xystrolepis* Tschudi, Fauna Peruana, Herp., p. 44. Type by monotypy: *Trachylepis punctata* Tschudi (cf. Dunn, 1936, Proc. Acad. Nat. Sci. Philadelphia, for 1935, **87**, p. 557).

1845. *Copeglossum* Tschudi, Fauna Peruana, Herp., p. 45. Type by monotypy: *C. cinctum* Tschudi = *Lacertus mabouya* Lacépède.

1845. *Chioninia* Gray, Cat. Lizards Brit. Mus., p. 116. Type by present designation: *Euprepes delalandii* Duméril & Bibron.

1848. *Elabites* Gistel, Naturg. Thierr., p. ix. Substitute name for *Euprepis* Wagler, 1830.

1925. *Mabuiopsis* Angel, Rept. et Batr. in "Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). Résultats scientifiques. Vertebrata." (Paris), **2**, p. 21. Type by monotypy *Mabuia Jeanneli* Angel = *M. irregularis* Lönnberg.

Mabuya quinquetaeniata obsti Werner

Tanganyika Five-lined Skink[50]

[50] Only females and young are five-lined and blue-tailed, the males are strikingly different. The number of midbody scale-rows enables this inhabitant of rocky outcrops to be broken up into several races, however the change is so gradual that the limits have to be somewhat arbitrarily defined. North of Uganda one encounters typical *M. q. quinquetaeniata* (Lichtenstein). South of the Zambezi is *M. q. margaritifer* (Peters), described from Tete, Mozambique (cf. Loveridge, 1953, Bull. Mus. Comp. Zool., **110**, pp. 196-200, 308).

1913. *Mabuia obsti* Werner, Jahrb. Hamburg. Wiss. Anst. for 1912, **30**, p. 43: Kwa Mtoro, Usandawi, Tanganyika Territory.

1917. *Mabuia quinquetaeniata hildebrandti* Sternfeld (not Peters:1874), Wiss. Ergebn. Deut. Zweiter Zentral-Afrika-Exped. 1910-1911, **1**, p. 438, pl. xxiv, fig. 3: "Taita," i.e. Teita, Kenya Colony.

Range. Uganda; Kenya Colony; Tanganyika Territory and Chapnani Island, Zanzibar (Tornier:1900), south through Nyasaland to the Zambezi.

Mabuya maculilabris maculilabris (Gray)[51]

Speckle-lipped Skink.

1845. *Euprepis maculilabris* Gray, Cat. Lizards Brit. Mus., p. 114: West Africa.

1866. *Euprepes anchietae* Bocage, Jorn. Sci. Lisboa, **1**, p. 62: "Zaire," i.e. Congo River.

1879. *Euprepes notabilis* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 36: Chinchoxo, Cabinda; and Pungo Ndongo, Angola.

1912. ?*Mabuia maculilabris major* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 232: Central Lake Region.

1912. *Mabuia maculilabris* var. *kwidjwiensis* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 233: "Kwidjwi" i.e. Idjwi Island, Lake Kivu, Belgian Congo.

1912. *Mabuia maculilabris* var. *wauensis* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 233: Wau Island, Lake Kivu, Belgian Congo.

1912. *Mabuia maculilabris* var. *schubotzi* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 233, pl. vi, fig. 3: Kisenyi, Lake Kivu, Belgian Ruanda-Urundi; and Fort Beni, Belgian Congo.

1912. *Mabuia maculilabris* var. *graueri* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 234, pl. vi, fig. 4: Kisenyi, Lake Kivu, Belgian Ruanda-Urundi; also the Aruwimi-Ituri region and between the Lualaba River and Lake Tanganyika, Belgian Congo.

1912. *Mabuia maculilabris* var. *rohrbecki* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 234: Nguru Mountains; also "Langenburg," i.e. Manda, Lake Nyasa, Tanganyika Territory.

[51] This species is much in need of critical study on a continental scale. *M. m. major*, designated as a subspecies by its author to distinguish it from the color varieties he named, appears to be a recognizable race, but when one attempts to define its range difficulties arise. Seemingly one must accept a great many forms based on average size and color (subject to fading), or reject them resolutely. In the Usambara Mountains and adjacent coast one meets with a robust and handsomely coloured form to which, rightly or wrongly, I have been applying the name "*comorensis* Peters."

1912. *Mabuia maculilabris* var. *bergeri* Sternfeld, Wiss. Ergebn. Dent. Zentral-Afrika-Exped. 1907-1908, **4**, p. 235: Dufile, Sudan.

Range. Chiefly savanna areas of the southern Sudan and ?? Somalia (*fide* Calabresi:1915), south through Uganda; Kenya Colony and Tanganyika Territory (for off-shore islands see races), west through Northern Rhodesia to Angola north and west to French Guinea.

Mabuya maculilabris comorensis (Peters)[52]

Comoro Speckle-lipped Skink

1854. *Euprepes comorensis* Peters, Monatsber. Akad. Wiss. Berlin, p. 619: "Anjuan," i.e. Johanna Island, Comoro Islands.

1882. *Euprepes angasijanus* Peters, Reise nach Mossambique, **3**, p. 73: Angasiya, Grand Comoro Island.

1913. *Mabuia comorensis* var. *infralineata* Boettger, in Voeltzkow, Reise in Ostafrika, **3**, p. 329: Europa Island, Mozambique Channel.

Range. Chiefly virgin forest, or recently deforested, areas of coastal Kenya Colony (Mombasa), south through Tanganyika Territory (Usambara and Uluguru Mountains) also Zanzibar, Mafia, Comoro and Europa Islands to Nyasaland (gallery forest along Ruo River, Mlanje Mountain). Possibly Northern Rhodesia (Meruwantipa).

Mabuya maculilabris albotaeniata Boettger[53]

Pemba Speckle-lipped Skink

1913. *Mabuia albotaeniata* Boettger, in Voeltzkow, Reise in Ostafrika, **3**, p. 350, pl. xxiv, figs. 1-2: Pemba Island.

Range. Pemba Island.

Mabuya maculilabris boulengeri Sternfeld[54]

Lindi Speckle-lipped Skink

1911. *Mabuia boulengeri* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 248: Makonde Plateau, Lindi Province, Tanganyika Territory.

Range. On tree-trunks in southeastern Tanganyika Territory (Kilwa to Mikindani, inland to Songea), also Nyasaland (Mtimbuka near Fort Johnston).

[52] See preceding footnote. Possibly the synonyms should be recognized.

[53] Examination of a cotype (M.C.Z. 33528) and a dozen other specimens from seven localities on Pemba, reveal that this is a constantly recognizable color form; this has led me to reverse my synonymizing of it in 1928.

[54] Its distribution suggests that *boulengeri* may be a full species; the exceptionally long tail is correlated with a more strictly arboreal life.

Mabuya brevicollis (Wiegmann)

1837. *Euprepes brevicollis* Wiegmann, Arch. Naturg., **3**, Abt. 1, p. 133: "Abyssinia," i.e. Ethiopia.

1837. *Euprepes pyrrhocephalus* Wiegmann, Arch. Naturg., **3**, Abt. 1, p. 133: Aschik Island, Red Sea, Arabia.

1856. *Tiliqua burtoni* Blyth, Journ. Asiatic Soc. Bengal, **24**, p. 306: "Somali Country."

1893. *Mabuya chanleri* Stejneger, Proc. U. S. Nat. Mus., **16**, p. 721: Tana River, Kenya Colony.

1895. *Mabuya tessellata* Anderson, Proc. Zool. Soc. London, p. 636, pl. xxxvi, fig. 2: near Aden (inferred from title), Arabia.

1905. *Mabuia Rothschildi* Mocquard, Bull. Mus. Hist. Nat. (Paris), **11**, p. 286: Endessa, 8° 40′ N., 40° E., Ethiopia.

1915. *Mabuya pulchra* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 29: "Lahadsch," i.e. Lahej, near Aden, Arabia.

Range. Sudan, east through Ethiopia and Eritrea to Aschik Island and Arabia, south through British Somaliland and Somalia to Uganda; Kenya Colony and Tanganyika Territory.

Mabuya planifrons (Peters)[55]

1878. *Euprepes* (*Euprepis*) *planifrons* Peters, Monatsb. Akad. Wiss. Berlin, p. 203, pl. ii, fig. 2: "Taita," i.e. Teita, Kenya Colony.

1878. *Euprepes* (*Euprepis*) *taitanus* Peters, Monatsb. Akad. Wiss. Berlin, p. 203, pl. ii, fig. 3: "Taita," i.e. Teita, Kenya Colony.

1911. *Mabuia diesneri* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 248: Kibwezi, Kenya Colony.

Range. Ethiopia, east to British Somaliland and Somalia, south through Kenya Colony to Tanganyika Territory.[55]

Mabuya megalura (Peters) Grass-top Skink

1878. *Euprepes* (*Mabuia*) *megalura* Peters, Monatsb. Akad. Wiss. Berlin, p. 204, pl. ii, fig. 4: "Taita," i.e. Teita, Kenya Colony.

1884. *Eumeces massaianus* Fischer, Jahrb. Hamburg, Wiss. Anst., **1**, p. 18, pl. ii, fig. 5: Lake Naivasha Highlands, Kenya Colony.

Range. Ethiopia and Somalia, south through Uganda; Kenya Colony and Tanganyika Territory to Belgian Ruanda-Urundi and the adjacent Belgian Congo.

Mabuya bayonii keniensis Loveridge Eastern Bayon's Skink[56]

[55] Specimens from northeast Tanganyika Territory are typical; in the remainder of the Territory southwest to Nyamkolo, Lake Tanganyika, Northern Rhodesia, they are intermediate towards *perrotetii* (Duméril & Bibron) as I have discussed elsewhere (1957, Tanganyika Notes & Records, No. 43, p. 4).

[56] East African skinks formerly referred to *bayonii* (Bocage), differ from that Angola species in possessing tricarinate scales. Possibly the eastern form extends to the Belgian Congo (Laurent:1952) and northeastern Angola.

1956. *Mabuya bayonii keniensis* Loveridge, Breviora (Cambridge, Mass.), No. 59, p. 2: Northern Uaso Nyiro, Sotik, Kenya Colony.

Range. Kenya Colony and Tanganyika Territory.[56]

Mabuya varia varia (Peters)[57] Savanna Variable Skink

1867. *Euprepes* (*Euprepis*) *varius* Peters, Monatsb. Akad. Wiss. Berlin, p. 20: Tete, Mozambique.

1867. *Euprepes Olivieri* var. *albo-punctatus* Bocage, Jorn. Sci. Lisboa, **1**, p. 223: Benguela and Catumbela, Angola.

1869. *Euprepes damaranus* Peters, Öfvers. Kongl. Vet.-Akad. Förh., p. 660: Damaraland, Southwest Africa.

1869. *Euprepes* (*Mabuya*) *laevigatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 434: Gerlachshoop, north of Middleburg, Transvaal.

1871. *Euprepes* (*Euprepis*) *Isselii* Peters, Monatsb. Akad. Wiss. Berlin, p. 567: "Keren," i.e. Cheren, Bogos, Eritrea.

1872. *Euprepes angolensis* Bocage, Jorn. Sci. Lisboa, **4**, p. 78: Bibala, Mossamedes; also Dondo, Angola.

1874. *Euprepes* (*Euprepis*) *hildebrandtii* Peters, Monatsb. Akad. Wiss. Berlin, p. 372, pl. —, fig. 4: "Barawa," i.e. Brava, Somalia.

Range. Sudan, east to British Somaliland, south through Uganda; Kenya Colony and Tanganyika Territory to Natal, west to Southwest Africa, north to Boma, Belgian Congo.

Mabuya varia brauni Tornier[58] Ukinga Montane Skink

1902. *Mabuia brauni* Tornier, Zool. Jahrb. Syst., **15**, p. 585: Ukinga Mountains, Tanganyika Territory.

Range. Tanganyika Territory (known only from the holotype).

Mabuya irregularis Lönnberg Alpine-meadow Skink

1922. *Mabuia* (*striata* ? var.) *irregularis* Lönnberg, Arkiv. Zool. **14**, No. 12, p. 4: Soy, Kenya Colony.

1923. *Mabuia Jeanneli* Angel, Bull. Mus. Hist. Nat. (Paris), **29**, p. 490: Mount Kinangop, Aberdare Mountains, Kenya Colony.

Range. Alpine meadows of Uganda (Mount Elgon) and Kenya Colony (Mounts Kinangop and Kenya).

[57] The Museum of Comparative Zoology has a cotype of *isselii* with 3 (instead of 1) frontoparietals. Parker's comments (1942, Bull. Mus. Comp. Zool., **91**, p. 84) notwithstanding, I think the status of *hildebrandtii* is more probably that of a synonym than a full species. Its distribution scarcely permits of its being a recognizable race. All the available material should be restudied.

[58] I am now inclined to think this skink may be a race of *bocagii* related to *M. b. mlanjensis* Loveridge of Nyasaland.

Mabuya striata striata (Peters)[59] Common Two-striped Skink

1844. *Tropidolepisma striatum* Peters, Ber. Akad. Wiss. Berlin, p. 36: Mozambique.

1849. *Euprepes punctatissimus* A. Smith, Illus. Zool. S. Africa, Rept., pl. xxxi, fig. 1: northeastern districts of Cape Province, South Africa.

1849. *Euprepes sunderallii* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 11: Interior of South Africa.

1864. *Euprepes grantii* Gray, Proc. Zool. Soc. London, p. 62: "South-Eastern Africa," i.e. Zambezi region.

1869. *Euprepes variegatus* Peters, Öfvers. Kongl. Vet.-Akad. Förh., p. 660: Damaraland, Southwest Africa.

1869. *Euprepes wahlbergii* Peters, Öfvers, Kongl. Vet.Akad. Förh., p. 661: Damaraland, Southwest Africa.

1869. *Euprepes* (*Euprepis*) *Grützneri* Peters, Monatsb. Akad. Wiss. Berlin, p. 433: Gerlachshoop, north of Middleburg, Transvaal.

Range. Ethiopia and British Somaliland, south through Uganda; Kenya Colony and Tanganyika (also Pemba; Zanzibar and Mafia Islands) to Natal, west to Southwest Africa, possibly north to the Belgian Congo.

Genus **RIOPA** Gray[60]

1839. *Riopa* Gray, Ann. Nat. Hist., **2**, p. 332. Type by subsequent designation: *Lacerta punctata* Linnaeus.

1839. *Chiamela* Gray, Ann. Nat. Hist., **2**, p. 332. Type by subsequent designation: *C. lineata* Gray.

1839. *Hagria* Gray, Ann. Nat. Hist., **2**, p. 333. Type by monotypy: *H. vosmaerii* Gray.[61]

1839. *Campsodactylus* Duméril & Bibron, Erpét. Gén., **5**, p. 761. Type by monotypy: *C. lamarrei* Duméril & Bibron = *Hagria vosmaerii* Gray.

1843. *Liosoma* Fitzinger (not of Brandt:1834), Syst. Rept., p. 22.

[59] This synonymy requires restudying and the range correlated with those of *M. s. ellenbergeri* Chabanaud of Zambezia, and the various forms described from Angola and Southwest Africa.

[60] Treated by Boulenger (1887, Cat. Lizards Brit. Mus., **3**, p. 220) as a "Section" of the genus *Lygosoma*. Subsequently, by common consent, raised to full generic status, an action confirmed by Malcolm A. Smith (1937, Rec. Indian Mus., **39**, p. 227). It is in this sense it is used here. More recently Mittleman (1952, Smithsonian Misc. Coll., **117**, No. 17, pp. 8-10, 18-21), in a survey of Lygosomine genera, has suggested further subdivision to a quite unacceptable degree. He divides *Riopa* into six full genera. Of the species listed here he would retain only *mabuiiformis* and *tanae*. To *Mochlus* he refers *fernandi, sundevallii, modesta* and *pembana*, reviving *Eumecia* for the reception of *anchietae*.

[61] *Scincus vosmaerii* Cocteau, which Gray cites as a synonym, appears to be only a manuscript name.

Type by original designation: *Eumeces microlepis* Duméril & Bibron.

1843. *Sphenosoma* Fitzinger, Syst. Rept., p. 23. Type by original designation: *Lacerta punctata* Linnaeus.

1843. *Eugongylus* Fitzinger, Syst. Rept., p. 23. Type by original designation: *Eumeces oppellii* Duméril & Bibron = *Lacerta rufescens* Shaw (part).

1864. *Mochlus* Günther, Proc. Zool. Soc. London, p. 308. Type by monotypy: *M. punctulatus* Günther = *Eumeces sundevallii* A. Smith.

1870. *Eumecia* Bocage, Jorn. Sci. Lisboa, **3**, p. 67. Type by monotypy: *E. anchietae* Bocage.

1880. *Scpacontias* Günther, Ann. Mag. Nat. Hist., (5) **6**, p. 235. Type by monotypy: *S. modestus* Günther.

1892. *Lepidothyris* Cope, Journ. Morph., **7**, p. 233. Type by subsequent designation: *Tiliqua fernandi* Burton.

1952. *Squamicilia* Mittleman, Smithsonian Misc. Coll., **117**, No. 17, p. 9. Type by original designation: *Eumeces isodactylus* Günther.

1952. *Tachygia* Mittleman, Smithsonian Misc. Coll., **117**, No. 17, p. 10. New name for *Liosoma* Fitzinger:1843 (preoccupied).

Riopa mabuiiformis Loveridge Mabuya-like Skink

1935. *Riopa mabuiiformis* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 12: Ngatana, Tana River, Kenya Colony.

Range. Kenya Colony (known only from the type series).

Riopa tanae Loveridge Tana-Delta Skink

1935. *Riopa tanae* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 11: Kau, near mouth of the Tana River, Kenya Colony.

Range. Coastal Kenya Colony.

Riopa fernandi (Burton) Red-and-black Skink

1836. *Tiliqua fernandi* Burton, Proc. Zool. Soc. London, p. 62: Fernando Po, Gulf of Guinea.

1845. *Plestiodon Harlani* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 170: Liberia.

1854. *Euprepis striata* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 98: Liberia.

1883. *Eupreprs* (*Tiliqua*) *elegans* J. G. Fischer (not of Peters:1854), Oester-Progr. Akad. Gymn. Hamburg, p. 3, pl. —, figs. 12-15: Sierra Leone.

1884. *Eupreprs leoninus* Fischer (new name for *elegans* Fischer, preoccupied), Abhand. Nat. Ver. Hamburg, **8**, p. 7.

1885. *Tiliqua nigripes* F. Müller, Verh. Naturf. Ges. Basel, **7**, p. 704: Gold Coast.

Range. Uganda and Belgian Ruanda-Urundi, west through Belgian Congo to French Guinea.

Riopa sundevallii sundevallii (Smith)[62]
Sundevall's Writhing-Skink

1849. *Eumices* (*Riopa*) *sunderallii* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 11: Country eastward of Cape Colony, i.e. Natal, South Africa.

1854. *Eumeces afer* Peters, Monatsb. Akad. Wiss. Berlin, p. 619: Mozambique Island; Boror; Inhambane and Mossimboa, Mozambique.

1862. *Eumeces reticulatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 23: New Barmen, Hereroland, Southwest Africa.

1864. *Mochlus punctulatus* Günther, Proc. Zool. Soc. London, p. 308: Zambezi Expedition.

1868. *Eumeces perdicicolor* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 317: Zanzibar Island.

1870. *Euprepes* (*Senira*) *Dumerili* Steindachner, Sitzb. Akad. Wiss. Wien, **62**, Abt. 1, p. 341, pl. iii, fig. 5: Zanzibar Island.

1898. *Lygosoma ferrandii* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova (2), **18**, p. 718, pl. ix, fig. 2: Lugh, Somalia.

Range. Sudan, east to French Somaliland (and Arabia), south through Uganda; Kenya Colony; Tanganyika Territory; Zanzibar and Mafia Islands to Natal, northwest through the Transvaal to Southwest Africa, north to French Equatorial Africa where one encounters intermediates with a western race.[63]

Riopa modesta modesta (Günther) Brown Writhing-Skink

1880. *Sepacontias modestus* Günther, Ann. Mag. Nat. Hist., (5) **6**, p. 235: Mpwapwa, Ugogo, Tanganyika Territory.

Range. Ethiopia (1895) and Uganda (1902), east and south through Kenya Colony and Tanganyika Territory direct to Nyasaland; also recorded from Belgian Ruanda-Urundi (1912), the Belgian Congo (1952) and Angola (1937).[64]

[62] Omissions from the synonymy refer to the western subspecies.

[63] *R. s. guineensis* (Peters:1879), erroneously recorded from East Africa by Tornier (1896), is a barely recognizable form on the basis of fewer subdigital lamellae beneath the fourth toe. It (including *chaperi* Chabanaud:1884) ranges from French Equatorial Africa (intermediates) west to Portuguese Guinea. In this connection the status of *houyi* (Sternfeld:1916) and *mocquardi* (Chabanaud: 1917) require investigating.

[64] The resemblance to *sundevallii* of occasional examples of *modesta* make it necessary to view with suspicion the five solitary records of its occurrence outside its customary range. British Somaliland records are referable to *R. m. somalica* Parker (1942).

Riopa pembana (Boettger) Pemba Island Writhing-Skink

1913. *Lygosoma* (*Riopa*) *pembanum* Boettger, in Voeltzkow, Reise in Ostafrika, **3**, p. 350, pl. xxiv, figs. 4-5: Pemba Island.

Range. Coastal Kenya Colony (probably introdueed) and Pemba Island.

Riopa anchietae (Bocage) Western Serpentiform Skink

1870. *Eumecia anchietae* Bocage, Jorn. Sci. Lisboa, **3**, p. 67, pl. i: Huilla Plateau, Mossamedes, Angola.

Range. Western Kenya Colony and Tanganyika Territory, southwest to Northern Rhodesia and Angola, north to Belgian Congo.

Genus **LYGOSOMA** Hardwicke & Gray[65]

1827. *Lygosoma* Hardwicke & Gray, Zool. Journ., **3**, p. 228. Type by monotypy: *Lacerta serpens* Bloch = *Anguis quadrupes* Linnaeus.

Subgenus **LEPTOSIAPHOS** Schmidt

1943. *Leptosiaphos* K. P. Schmidt, Field Mus. Nat. Hist. Zool. Ser., **24**, p. 332. Type by original designation: *Lygosoma meleagris* Boulenger.

Lygosoma kilimense Stejneger[66] Kilimanjaro Five-toed Skink

1891. *Lygosoma kilimensis* Stejneger, Proc. U. S. Nat. Mus., **14**, p. 405: Mount Kilimanjaro, Tanganyika Territory.

1900. *Lygosoma clathrotis* Boulenger, Ann. Mag. Nat. Hist., (7) **6**, p. 194: foot of Mount Kenya, Kenya Colony.

1903. *Lygosoma thomasi* Tornier, Zool. Jahrb. Syst., **19**, p. 175: Nairobi, Kenya Colony.

1907. *Lygosoma aloysii-sabaudiae* Peracca, Boll. Mus. Zool. Anat. Comp. Univ. Torino, **22**, No. 553, p. 1: Mitiana and Toro, Uganda.

[65] Departing from the custom employed elsewhere, I have omitted the lengthy and questionable synonymy of *Lygosoma*. Its East African representatives all belong to the subgenus *Leptosiaphos*, separated by Schmidt from *Saiphos* (correct spelling) of Gray:1831 whose range is restricted to southeast Asia and Australia. Mittleman (1952, Smithsonian Misc. Coll., **117**, No. 17, pp. 6, 20) regards *Leptosiaphos* as a full genus, separating it from *Saiphos* on characters I have had tested on 4 African species (177 specimens) and 6 Australian (22 specimens), and I found the following to hold good.

Ear-opening present though often minute; anal not or but slightly enlarged; range: East and Central Africa ..... *Leptosiaphos*
Ear-opening absent; anal noticeably enlarged; range: Malaya; Indonesia; Australia ..... *Saiphos*

[66] De Witte, who subsequently (1953) secured 182 of these skinks, concurs with my action in synonymizing *dewittei*. *L. gromleri*, referred by its author to *Riopa*, had a longitudinally divided frontonasal and so simulated a pair of supranasals; its synonymizing with *kilimensis* can be regarded as provisional.

1925. ?*Lygosoma gromieri* Angel, Bull. Mus. Hist. Nat. (Paris), **31**, p. 419: (On termitarium near station) Tsavo, Kenya Colony.

1933. *Lygosoma* (*Siaphos*) *compressicauda* Witte (not Werner: 1897), Revue Zool. Bot. Afr., **23**, p. 175, figs. 1-4: Sandoa, Belgian Congo.

1934. *Siaphos dewittei* Loveridge (new name for *compressicauda* Witte, preoccupied), Copeia, p. 184.

1943. *Lygosoma* (*Leptosiaphos*) *weberi* K. P. Schmidt, Field Mus. Nat. Hist. Zool. Ser., **24**, p. 335, fig. 27: Lotti Forest at about 3300 feet on west side of Imatong Mountains, Sudan.

Range. Virgin forest, usually on mountains, from southern Sudan through Uganda; Kenya Colony and Tanganyika Territory, west through the Belgian Congo to Congulu, Angola.

Lygosoma kutuense Lönnberg Kenya Five-toed Skink

1911. *Lygosoma kutuensis* Lönnberg, Kungl. Svenska. Vetensk.-Akad. Handl., **47**, No. 6, p. 17 fig. 3: Near Kutu Village, between Embu and Fort Hall, Kenya Colony.

Range. Kenya Colony (known only from the holotype).

Lygosoma graueri graueri Sternfeld Ruanda Five-toed Skink

1912. *Lygosoma graueri* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 240, fig. 3: Locality given only for races, so suggest restricting it to bamboo forest at foot of Mount Karisimbi, Belgian Ruanda-Urundi.

1912. *Lygosoma graueri quinquedigitata* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 241, fig. 3b, pl. vi, fig. 5: Bamboo forest at foot of Mount Karisimbi, Belgian Ruanda-Urundi.

Range. Virgin forests of Uganda; Belgian Ruanda-Urundi and the adjacent Belgian Congo.

Lygosoma meleagris Boulenger[67] Ruwenzori Four-toed Skink

1907. *Lygosoma meleagris* Boulenger, Ann. Mag. Nat. Hist., (7) **19**, p. 488: Mubuku Valley, 7000 feet, Ruwenzori Mountains, Uganda.

1932. *Siaphos meleagris helleri* Loveridge, Proc. Biol. Soc. Washington, **45**, p. 113: Bugongo Ridge, 9500 feet, Ruwenzori Mountains, Belgian Congo (*not* Uganda side).

1933. *Lygosoma* (*Siaphos*) *Burgeoni* de Witte, Revue Zool. Bot. Afr., **24**, p. 116, figs. 1-2: Kalonge, 6725 feet, Ruwenzori Mountains, Belgian Congo.

1941. *Lygosoma meleagris hackarsi* de Witte, Inst. Parcs Nat. Congo Belge, Expl. Parc Nat. Albert, Miss. G. F. de Witte (1933-

[67] Dr. de Witte (1953) concurs with the synonymy as given here.

1935), **33,** p. 138, figs. 39-40, pl. ii, figs. 4-6: Kamatembe, 6825 feet, Parc National Albert, Belgian Congo.

Range. Virgin forests of Uganda; Belgian Ruanda-Urundi and the adjacent Belgian Congo.

Genus **ABLEPHARUS** Fitzinger[68]

1823. *Ablepharus* Fitzinger, in Lichtenstein, Verz. Doubl. Zool. Mus. Berlin, p. 103. Type by monotypy: *A. pannonicus* Fitzinger.

1833. *Lerista* Bell, Proc. Zool. Soc. London, p. 99. Type by monotypy: *L. lineata* Bell.

1834. *Cryptoblepharum* (*sic*) Wiegmann, Herp. Mexicana, p. 12. Type by subsequent designation: *Ablepharus poecilopleuro* (*sic*) Wiegmann.

1839. *Petia* Gray, Ann. Nat. Hist., **2,** p. 335. Substitute name for "*Cryptoblepharus* Wiegmann."

1843. *Microblepharis* Fitzinger, Syst. Rept., p. 23. Type by original designation: *Ablepharus menestriesii* Duméril & Bibron = *Scincus bivittatus* Menestries.

1843. *Ophiopsis* Fitzinger, Syst. Rept., p. 23. Type by original designation: *Lerista lineata* Bell.

1845. *Morethia* Gray, Cat. Lizards Brit. Mus., p. 65. Type by monotypy: *M. anomalus* Gray.

1845. *Menetia* Gray, Cat. Lizards Brit. Mus., pp. 65, 66. Type by monotypy: *M. greyii* Gray.

1845. *Miculia* Gray, Cat. Lizards Brit. Mus., p. 66. Type by monotypy: *M. elegans* Gray.

1872. *Blepharosteres* Stoliczka, Proc. Asiatic Soc. Bengal, p. 74. Type by monotypy: *B. grayanus* Stoliczka.

1881. *Phaneropis* Fischer, Arch. Naturg., **47,** Abt. 1, p. 236. Type by monotypy: *P. muelleri* Fischer.

Ablepharus boutonii africanus Sternfeld

Coral-rag Snake-eyed Skink

1918. *Ablepharus boutoni africanus* Sternfeld, Abhand. Senckenberg. Nat. Ges., **36,** p. 423: Manda Island and Malindi, Kenya Colony; Pemba Island.

Range. Rocky coastal stretches of Somalia; Kenya Colony (including Manda, Lamu and Mombasa Islands); and Tan-

[68] Recently Mittleman (1952, Smithsonian Misc. Coll., **117,** No. 17, pp. 15, 19), following Stejneger, has revived *Crytoblepharus* as a full genus on the basis of its frontoparietal being fused with the interparietal, together with the size of its ear-opening. To me this seems a wholly unnatural division (cf. footnote to *A. wahlbergii*). It is customary to cite "Herp. Mexicana" for *Cryptoblepharus,* but Wiegmann gives *Cryptoblepharum* as a synonym of *Ablepharus* without intention of proposing a new genus.

ganyika Territory; also Pemba, Zanzibar and Mafia Islands.

Ablepharus wahlbergii (Smith)[69] Savanna Snake-eyed Skink

1849. *Cryptoblepharus wahlbergii* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 10: Natal, South Africa.

1894. *Ablepharus carsonii* Boulenger, Proc. Zool. Soc. London, p. 735, pl. xlix, figs. 4-4a: "Fwambo," i.e. Fwamba, Northern Rhodesia.

1924. *Ablepharus massaiensis* Angel, Bull. Mus. Hist. Nat. Paris, **30**, p. 52: Masai Plains near Nairobi, Kenya Colony.

Range. Ethiopia and British Somaliland, south through Somalia, Kenya Colony and Tanganyika Territory (reported from Grave Island, Zanzibar, but possibly in error for *boutonii africanus;* also Mafia Island) to Natal, west to Southwest Africa, northeast through Angola to Belgian Congo. Unknown from Uganda.

Ablepharus megalurus Nieden Blue-tailed Snake-eyed Skink

1913. *Ablepharus megalurus* Nieden, Mitt. Zool. Mus. Berlin, **7**, p. 89: "Kinjanganja in Turu, 4° 50′ S." i.e. Unyanganyi, Turu, Tanganyika Territory.

Range. Central Tanganyika Territory (from Unyanganyi south to Saranda on the Central Railway).

Genus **SCELOTES** Fitzinger[70]

1826. *Scelotes* Fitzinger, Neue Class, Rept., pp. 23, 53. Type by monotypy: *Bipes anguineus* Merrem = *Anguis bipes* Linnaeus.

1830. *Zygnis* Wagler (not Oken:1816), Nat. Syst. Amphib., p. 160. Type by monotypy: *Anguis bipes* Linnaeus.

1839. ?*Herinia* Gray, Ann. Mag. Nat. Hist., **2**, p. 332. Type by monotypy:

[69] *A. carsonii* is only tentatively referred to the synonymy. It was based on a single skink whose interparietal was fused with the frontoparietal, probably an individual aberration as *wahlbergii* is common at Abercorn, from which Fwamba is not very distant. The status of *A. tancredi* Boulenger (1909) from Dabarlf, Ethiopia, and *A. wilsoni* Werner (1914) from Talodl, Sudan, also merit investigation as both are still known only from their respective holotypes.

[70] Overlooking *Gongylomorphus* of Fitzinger, Witte & Laurent (1943, Mem. Mus. Royal Hist. Nat. Belgique, (2) Fasc. 26, p. 3) revived its synonym *Thyrus* as a monotypic genus.

They described *Proscelotes* for the reception of two species (*eggeli* and *uluguruensis*) possessing a frontal whose lateral borders are impinged upon by the first supraoculars. This character holds good for every individual in our fairly extensive representation of the two species in question, so that *Proscelotes* might be regarded as a recognizable subgenus.

So far as this check list is concerned, Witte & Laurent would refer the two forms of *tetradactylus* to *Scpsina* which, together with *Herpetosaura* they raise to full generic rank, while synonymizing *Melanoseps* with *Scelotes*. A multiplicity of small genera emphasizes differences at the expense of relationships, though in this instance the authors claim that similarities are the result of convergences.

H. capensis Gray, which therefore antedates *Gongylus capensis* sp. n. of A. Smith:1849.[71]

1839. *Amphiglossus* Duméril & Bibron, Erpét. Gén., **5**, pp. 606, 608. Type by monotypy: *A. astrolabi* Duméril & Bibron.

1843. *Gongylomorphus* Fitzinger, Syst. Rept., p. 22. Type by monotypy: *Scincus bojerii* Desjardin.

1845. *Thyrus* Gray, Cat. Lizards Brit. Mus., p. 124. Type by monotypy: *Scincus bojerii* Desjardin.

1849. *Lithophilus* A. Smith (not of Frölich:1799), Illus. Zool. S. Africa, Rept., App., p. 12. Type by subsequent designation: *L. inornatus* A. Smith.

1854. *Herpetosaura* Peters, Monatsb. Akad. Wiss. Berlin, p. 619. Type by monotypy: *H. arenicola* Peters.

1861. *Sepomorphus* Peters, Monatsb. Akad. Wiss. Berlin, p. 422. Type by monotypy: *S. caffer* Peters.

1866. *Sepsina* Bocage, Jorn. Sci. Lisboa, **1**, p. 62. Type by monotypy: *S. angolensis* Bocage.

1866. *Dumerilia* Bocage, Jorn. Sci. Lisboa, **1**, p. 63. Type by monotypy: *D. bayonii* Bocage.

1874. *Rhinoscincus* Peters, Monatsb. Akad. Wiss. Berlin, p. 374. Type by monotypy: *Sepsina* (*Rhinoscincus*) *tetradactyla* Peters.

1875. *Scincodipus* Peters, Monatsb. Akad. Wiss. Berlin, p. 551. Type by monotypy: *S. congicus* Peters = *Dumerilia bayonii* Bocage.

1887. *Herpetoseps* Boulenger, Cat. Lizards Brit. Mus., **3**, p. 416. Type by monotypy: *H. anguincus* Boulenger.

1943. *Prosceloles* Witte & Laurent, Mem. Mus. Royal Hist. Nat. Belgique, (2) Fasc. 26, pp. 9, 13. Type by original designation: *Scelotes eggeli* Tornier.

Scelotes eggeli Tornier Usambara Five-toed Scelotes

1902. *Scelotes eggeli* Tornier, Zool. Anz., **25**, p. 700: Kwai, western Usambara Mountains, Tanganyika Territory.

Range. Usambara Mountains Tanganyika Territory.

Scelotes uluguruensis Barbour & Loveridge
Uluguru Five-toed Scelotes

1928. *Scelotes uluguruensis* Barbour & Loveridge, Mem. Mus. Comp.

[71] From the brief description, Dr. V. FitzSimons considers that *H. capensis* may well be a *Scelotes*. Mr. J. C. Battersby writes me that the type of *H. capensis* Gray, 1838, is not to be found in the British Museum, and apparently was not there in 1887 when Boulenger wrote the Cat. Lizards Brit. Mus., **3**, p. 209 and listed "?*Herinia*" in the synonymy of *Lygosoma*. In 1935 Malcolm Smith (Fauna Brit. India, Rept. Amph., **2**, p. 216) transferred it to the synonymy of *Mabuya*, possibly on the assumption that it was identical with *Tiliqua capensis* Gray, 1830, which was also described from the Cape of Good Hope. The latter species, as *Mabuya capensis* (Gray), 1830, is in general use for *Scincus trivittatus* Cuvier, 1829, preoccupied by *trivittatus* Hardwicke & Gray.

Zool., **50**, p. 167, pl. iv, fig. 6: Bagilo, 5000 feet, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains, Tanganyika Territory.

Scelotes tetradactylus tetradactylus (Peters)
Eastern Four-toed Scelotes

1874. *Sepsina* (*Rhinoscincus*) *tetradactyla* Peters, Monatsb. Akad. Wiss. Berlin, p. 374: "Zanzibar Coast," i.e. Tanganyika Territory.

Range. Eastern Tanganyika Territory, south to Nyasaland.

Scelotes tetradactylus hemptinnei (Witte)
Western Four-toed Scelotes

1933. *Sepsina Hemptinnei* de Witte, Revue Zool. Bot. Afr., **23**, p. 188: Lukafu, Kundelungu, Katanga, Belgian Congo.

Range. Near Ujiji, Tanganyika Territory, west to Belgian Congo.

Genus **MELANOSEPS** Boulenger[72]

1887. *Melanoseps* Boulenger, Cat. Lizards Brit. Mus., **3**, p. 422. Type by monotypy: *Herpetosaura atra* Günther.

Melanoseps ater longicauda Tornier
Long-tailed Limbless-Skink

1900. *Melanoseps ater* var. *longicauda* Tornier, Zool. Jahrb. Syst., **13**, p. 602: Masailand, and "Karagwe am Pangani," i.e. Korogwe, Pangani River, Tanganyika Territory.

Range. Southern Kenya Colony and northern Tanganyika Territory (whether the skink from Uluguru Mountains should be included is uncertain).

Melanoseps ater rondoensis Loveridge
Rondo-Plateau Limbless-Skink

1942. *Melanoseps ater rondoensis* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 360: Nchingidi, 2700 feet, Rondo Plateau, Lindi District, Tanganyika Territory.

Range. Rondo Plateau, Tanganyika Territory.

[72] To the synopsis of the races furnished by me (1942, Bull. Mus. Comp. Zool., **91**, p. 359) should be added the Nyasaland forms described (1943, Bull. Mus. Comp. Zool., **110**, pp. 220-223).

Witte & Laurent (1943, Mem. Mus. Royal Hist. Nat. Belgique (2), Fasc. 26, p. 32) may well be right in merging *Melanoseps* with *Scelotes* but the decision merits careful revisionary study of the entire complex. These limbless skinks are associated with primary forest, either montane or gallery.

Melanoseps ater matengoensis Loveridge
Matengo-Highlands Limbless-Skink

1942. *Melanoseps ater matengoensis* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 361: Ugano, Matengo Highlands west of Songea, Tanganyika Territory.

Range. Matengo Highlands, Tanganyika Territory.

Melanoseps ater uzungwensis Loveridge
Uzungwe-Mountains Limbless-Skink

1942. *Melanoseps ater uzungwensis* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 361: Kigogo, Uzungwe Mountains, Tanganyika Territory.

Range. Uzungwe Mountains, Tanganyika Territory.

Genus **SCOLECOSEPS** Loveridge

1920. *Scolecoseps* Loveridge, Proc. Zool. Soc. London, p. 159. Type *S. boulengeri* Loveridge.

Scolecoseps acontias (Werner) Sandy-soil Limbless-Skink

1913. *Melanoseps acontias* Werner, 1912, Jahrb. Hamburg. Wiss. Anst. for 1912, **30**, p. 19: Dar es Salaam, Tanganyika Territory.

Range. Coastal (Dar es Salaam to Kilwa) Tanganyika Territory.

Genus **ACONTIAS** Cuvier

1817. *Acontias* Cuvier, Règne Animal, **2**, p. 60. Type by monotypy: *Anguis meleagris* Linnaeus.

Acontias percivali Loveridge Teita Mountains Limbless-Skink

1935. *Acontias percivali* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 13: Foot of Mount Mbololo, Teita Mountains, Kenya Colony.

Range. Vicinity of Voi, Kenya Colony

Genus **FEYLINIA** Gray

1845. *Feylinia* Gray, Cat. Lizards Brit. Mus., p. 129. Type by monotypy: *F. currori* Gray.

1856. *Anclytrops* A. Duméril, Revue Mag. Zool., (2) **8**, p. 420. Type by monotypy: *Acontias elegans* Hallowell.

1857. *Sphenorhina* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 52. Type by monotypy: *Acontias elegans* Hallowell.

1943. *Chabanaudia* Witte & Laurent, Mem. Mus. Royal Hist. Nat. Belgique, (2) Fasc. 26, p. 37. Type by original designation: *Feylinia boulengeri* Chabanaud.

Feylinia currori elegans (Hallowell)[73]
Western-Forest Limbless-Skink

1852. *Acontias elegans* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 65: "Liberia," probably in error for Gabon.

Range. Uganda (Entebbe; Sesse Islands, etc.) and western Tanganyika Territory (Bukoba), west through the Belgian and French Congo.

Family CORDYLIDAE (inc. GERRHOSAURIDAE)[74]

Genus **CORDYLUS** Laurenti

1763. *Cordylus* Gronovius, Zoophyl. Gronov. . . ., p. 13. (A work specifically rejected for taxonomic purposes in rule 89 of the Internat. Comm. Zool. Nomencl. — cf. 1926, Proc. Biol. Soc. Washington, **39**, p. 103).

1768. *Cordylus* Laurenti (part), Syn. Rept., p. 51. Type by devious tautonomy: *C. verus* Laurenti = *Lacerta cordylus* Linnaeus.

1820. *Zonurus* Merrem, Vers. Syst. Amphib., p. 57. Type by monotypy: *Lacerta cordylus* Linnaeus.

Cordylus cordylus tropidosternum (Cope)
Eastern Spiny-tailed Lizard

1869. *Zonurus tropidosternum* Cope, Proc. Amer. Philos. Soc., **11**, p. 169: "Madagascar" (presumably error for Mozambique).

1889. *Zonurus frenatus* Pfeffer, Jahrb. Hamburg. Wiss. Anst., **6**, p. 6: Mhonda, Eastern Province, Tanganyika Territory.

1934. *Zonurus parkeri* Cott, Proc. Zool. Soc. London, p. 151, pl. ii: Amatongas, Mozambique.

Range. Coastal Kenya Colony (near Malindi), south through Tanganyika Territory; Mozambique and Nyasaland to Southern Rhodesia (where it meets with *C. c. jonesii* and *C. c. rhodesianus*).

Cordylus ukingensis (Loveridge) Ukinga Spiny-tailed Lizard

1932. *Zonurus ukingensis* Loveridge, Bull. Mus. Comp. Zool., **73**, p. 378, pl. iii, fig. 2: Tandala, Ukinga, Tanganyika Territory.

Range. Southern Highlands of Tanganyika Territory.

[73] Witte and Laurent (1943) make this a full species. The genus is in great need of comprehensive revision based on *all* available material. Our Entebbe specimen has the ocular in contact with the second labial; also 26 midbody scale-rows.

[74] McDowell and Bogert (1954, Bull. Am. Mus. Nat. Hist., **105**, pp. 98-102) have advanced reasons for the merging of these two families. For synonymy of family names see Loveridge, 1957, Tanganyika Notes & Records, No. 43, p. 6.

Genus **GERRHOSAURUS** Wiegmann

1828. *Gerrhosaurus* Wiegmann, Isis von Oken, p. 378. Type by monotypy: *G. flavigularis* Wiegmann.

1836. *Pleurotuchus* A. Smith, Mag. Zool. Bot. (Jardine), **1**, p. 142. Type by monotypy: *P. typicus* Smith.

1837. *Pleurotychus* Wiegmann, Arch. Naturg., **3**, Abt. 2, p. 228. Emendation for *Pleurotuchus* A. Smith.

Gerrhosaurus major bottegoi Prato[75]

Eritrean Great Plated-Lizard

1895. *Gerrhosaurus bottegoi* del Prato, Atti, Soc. Ital. Sci. Nat. (Milano), **35**, p. 19, figs. 1-1a: Ghinda Valley, Eritrea.

Range. Eritrea, south through Ethiopia and Somalia to Kenya Colony and central Tanganyika Territory.

Gerrhosaurus major major Duméril

Zanzibar Great Plated-Lizard

1851. *Gerrhosaurus Major* A. Duméril, Cat. Méthod. Coll. Rept. Mus. Paris, p. 139: Zanzibar Island.

1889. *Gerrhosaurus zanzibaricus* Pfeffer, Jahrb. Hamburg. Wiss. Anst., **6**, p. 7: "Kibueni," i.e. Kibweni, Zanzibar Island.

1906. *Gerrhosaurus bergi* Werner, Zool. Anz., **30**, p. 54, figs. 1-3: Usambara Mountains, Tanganyika Territory.

Range. Eastern Kenya Colony; Tanganyika Territory and Zanzibar Island, south to northern Mozambique (at Lumbo and Tete).

Gerrhosaurus major grandis Boulenger[76]

Zululand Great Plated-Lizard

1908. *Gerrhosaurus grandis* Boulenger, Ann. Natal Mus., **1**, p. 225, pl. xxxvi: Zululand, Natal.

Range. Central (Morogoro) and southeast (Kilwa; Liwale; Tunduru) Tanganyika Territory, south through Mozambique (Amatongas) and the Rhodesias to Transvaal and Natal.

Gerrhosaurus nigrolineatus nigrolineatus Hallowell

Black-lined Plated-Lizard

1857. *Gerrhosaurus nigro-lineatus* Hallowell, Proc. Acad. Nat. Sci. Phila-

[75] East African records of *G. m. zechi* Tornier should be referred to *m. bottegoi*, as *m. zechi* is the somewhat darker form ranging from the southern Sudan and Belgian Congo west to Togo.

[76] The extensive area of overlap with *G. m. major* is admitted and correct; it needs to be worked out in detail if *m. grandis* — apparently readily recognisable in the south — is to be maintained.

delphia, p. 49: Gabon, French Congo.

1866. *Gerrhosaurus multilineatus* Bocage, Jorn. Sci. Lisboa, **1**, p. 44: Duque de Braganca, Mossamedes, Angola.

1907. *Gerrhosaurus flavigularis* forma *intermedia* Lönnberg, in Sjöstedt, Wiss. Ergeb. Schwed. Zool. Exped. Kilimanjaro, Meru umbeg. Massaisteppen, No. 4, p. 7, pl. i, figs. 1a-1b: steppe near Lake Natron, northern Tanganyika Territory.

1939. *Gerrhosaurus nigrolineatus australis* FitzSimons, Ann. Transvaal Mus., **20**, p. 10: Kaapmuiden, eastern Transvaal.

Range. Kenya Colony and Tanganyika Territory, south to the Transvaal, west to Southwest Africa, north to the French Congo.

Gerrhosaurus flavigularis fitzsimonsi Loveridge

Kenya Yellow-throated Plated-Lizard

1942. *Gerrhosaurus flavigularis fitzsimonsi* Loveridge, Bull. Mus. Comp. Zool., **89**, p. 514: Mount Mbololo, Teita, Kenya Colony.

Range. Eastern Sudan and Ethiopia south through Kenya Colony to southern Tanganyika Territory. ? "Zanzibar."

Genus **TETRADACTYLUS** Merrem

1820. *Tetradactylus* Merrem (not Duméril & Bibron ms. Paris Mus.), Vers. Syst. Amph., pp. 13, 75. Type by tautonomy: *Chalcides tetradactylus* Daudin.

1825. *Cicigna* Gray, Ann. Philos., (2) **10**, p. 201. Type by monotypy: *Scincus sepiformis* Schneider = *Lacerta seps* Linnaeus.

1826. *Saurophis* Fitzinger, Neue Class. Rept., pp. 20, 50. Type by monotypy: *Lacerta seps* Linnaeus.

1838. *Caitia* Gray, Ann. Nat. Hist., **1**, p. 389. Type by monotypy: *C. africana* Gray.

1843. *Homodactylus* Fitzinger, Syst. Rept., p. 22. Type by original designation: *Caitia africana* Gray.

1845. *Pleurostrichus* Gray, Cat. Lizards Brit. Mus., p. 51. Type by present designation: *Scincus sepiformis* Schneider = *Lacerta seps* Linnaeus.

1892. *Caetia* Cope, Journ. Morph., **7**, p. 224. Emendation for *Caitia* Gray:1838.

Tetradactylus fitzsimonsi simplex Laurent

Congo Long-tailed Seps

1950. *Tetradactylus fitzsimonsi simplex* Laurent, Revue Zool. Bot. Afr., **43**, p. 350: Kundelungu, 1750 metres, Belgian Congo.

Range. Southeastern Tanganyika Territory, west through Northern Rhodesia to eastern Belgian Congo.

Genus **CHAMAESAURA** Schneider

1801. *Chamaesaura* Schneider (part), Hist. Amphib., **2**, pp. 205, 210. Type by designation of Fitzinger:1826: *Lacerta anguina* Linnaeus.

1820. *Monodactylus* Merrem, Vers. Syst. Amphib., pp. 13, 76. Type by monotypy: *Lacerta anguina* Linnaeus.

1832. *Crieochalcis* Wiegmann, Handbuch Zool., p. 185. Type by monotypy: *C. aenea* Weigmann.

1862. *Mancus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 339. Type by monotypy: *M. macrolepis* Cope.

Chamaesaura anguina tenuior Günther Uganda Snake-Lizard

1895. *Chamaesaura tenuior* Günther, Ann. Mag. Nat. Hist., (6) **15**, p. 524, pl. xxi, fig. B: Kampala, Uganda.

1899. *Chamaesaura annectens* Boulenger, Proc. Zool. Soc. London, p. 97: Ravine Station, 7500 feet, Mau Mountains, Kenya Colony.

Range. Grasslands of eastern Belgian Congo, east through Uganda and Kenya Colony to the Usambara Mountains, Tanganyika Territory.

Chamaesaura miopropus Boulenger Northern Rhodesia Snake-Lizard

1894. *Chamaesaura miopropus* Boulenger, Proc. Zool. Soc. London, pp. 724, 732: "Fwambo," i.e. Fwamba, Northern Rhodesia.

Range. Grasslands of southern Tanganyika Territory, west through Northern Rhodesia to Angola.

Family LACERTIDAE[77]

Genus **GASTROPHOLIS** Fischer

1886. *Gastropholis* Fischer, Abhand. Nat. Ver. Hamburg, **9**, p. 1. Type by monotypy: *G. vittata* Fischer.

Gastropholis vittata Fischer Keel-bellied Ground-Lizard

1886. *Gastropholis vittata* Fischer, Abhand. Nat. Ver. Hamburg, **9**, p. 1, pl. i, fig. 1: "Zanzibar," probably coast of opposite mainland.

1900. *Gastropholis lutzei* Tornier, Zool. Jahrb. Syst., **13**, p. 591, fig. —: Tanga, Tanganyika Territory.

[77] In his revision of this family, Boulenger (1920, Monog. Lacertidae, **1**, p. 2) stressed the difficulties attending any attempt to arrange the genera in a linear sequence. He placed *Nucras* at the head of the list in the belief that it dated from the Oligocene. This idea arose from a specimen preserved in what was thought to be Baltic amber, whereas it was almost certainly in so-called "Zanzibar copal" from the Tanganyika coastlands.

1904. *Gastropholis prasina* Werner, Zool. Anz., **27**, p. 462: Tanganyika Territory (as Kleeberg coll., probably Tanga).

Range. Coastal Tanganyika Territory and Mozambique (at Lumbo, unless separable). No definite record from Zanzibar Island.

Genus **BEDRIAGAIA** Boulenger

1916. *Bedriagaia* Boulenger, Ann. Mag. Nat. Hist., (8) **18**, p. 112. Type by monotypy: *B. tropidopholis* Boulenger.

Bedriagaia moreaui Loveridge. Keel-bellied Tree-Lizard

1936. *Bedriagaia moreaui* Loveridge, Proc. New England Zool. Club, **15**, p. 67, figs. —: Amani, Usambara Mountains, Tanganyika Territory.

Range. Tanganyika Territory (a canopy-dwelling species known only from the holotype and a second specimen found in the middle of Tanga township, so R. E. Moreau informs me — 6.ix.1944).

Genus **HOLASPIS** Gray

1863. *Holaspis* "A. Smith" Gray, Proc. Zool. Soc. London, p. 152. Type by monotypy: *H. guentheri* Gray.

Holaspis guentheri laevis Werner
Eastern Serrate-toed Tree-Lizard

1895. *Holaspis guentheri laevis* Werner, Verh. Zool. Bot. Ges. Wien, **45**, p. 191, pl. v, fig. 4: Usambara Mountains, Tanganyika Territory.

Range. Northeast Tanganyika Territory, south to Amatongas, Mozambique.

Holaspis guentheri guentheri Gray
Western Serrate-toed Tree-Lizard

1863. *Holaspis guentheri* "A. Smith" Gray, Proc. Zool. Soc. London, p. 153, pl. xx, fig. 1: No locality.

Range. Uganda, southwest to Angola, northwest to Sierra Leone.

Genus **PHILOCHORTUS** Matschie

1893. *Philochortus* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 30. Type by monotypy: *P. neumanni* Matschie.

Philochortus intermedius rudolfensis Parker
Southern Shield-backed Ground-Lizard

1932. *Philochortus intermedius rudolfensis* Parker, Journ. Linn. Soc. London, Zool., **38**, p. 226: near mouth of Kaliokwell River, Lake Rudolf, Kenya Colony.

Range. Northern Kenya Colony (known only from the holotype).

Genus **ALGYROIDES** Bibron[78]

1833. *Algyroides* Bibron, in Bory de St. Vincent, Expéd. Sci. Morée Rept., p. 67. Type by monotypy: *A. moreoticus* Bibron.

1834. *Notopholis* Wiegmann (not Weigmann:1830), Herp. Mexicana, p. 10. Type by monotypy: *N. fitzingeri* Wiegmann.

1843. *Tropidopholis* Fitzinger, Syst. Rept., p. 21. New name for *Notopholis* Wiegmann:1834.

1868. *Endromius* Gistel, in Blicke, Leben Natur Menschen (Leipzig) p. 150. Type (*fide* Mertens:1936): *Algyroides moreoticus* Bibron.

1912. *Adolfus* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 220. Type by present designation: *A. fridericianus* Sternfeld = *Algyroides africanus* Boulenger.

Algyroides alleni Barbour Alpine-meadow Lizard

1914. *Algiroides alleni* Barbour, Proc. New England Zool. Club, **4**, p. 97: northeast slope of Mount Kenya, Kenya Colony.

Range. Above 9000 feet on mountains of Uganda (Elgon) and Kenya Colony (Aberdares; Kenya; Kinangop).

Algyroides africanus Boulenger Multi-scaled Forest-Lizard

1906. *Algiroides africanus* Boulenger, Proc. Zool. Soc. London, **2**, p. 570, fig. 96: Entebbe, Uganda.

1912. *Adolfus fridericianus* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 220, figs. 1 and 2b: Avakubi, upper Aruwimi River, Belgian Congo.

Range. Uganda, west through the Belgian Congo to French Cameroon.

[78] This name was proposed in a volume that appeared in 1833-1835. Sherborn gives 1833 for *Algyroides*, but Boulenger cites 1835, using the amended spelling (*Algiroides*) proposed by Duméril & Bibron, 1839, Erpét. Gén. **5**, pp. 174, 192.

Notopholis was first proposed by Wiegmann in 1830 to replace his preoccupied *Apistes*, of which the type was *Lacerta edwarsiana* Dugés = *Psammosaurus hispanicus* Fitzinger. Consequently *Notopholis* Wiegmann, 1834, is a preoccupied homonym.

Algyroides vaucreselli (Tornier) Sparser-scaled Forest-Lizard

1902. *Lacerta vaucreselli* Tornier, Zool. Anz., **25**, p. 701: Kagera, west of Lake Victoria, Tanganyika Territory.

1917. *Algiroides Boulengeri* Peracca, Atti Accad. Sci. Torino, **52**, p. 351: Fort Portal, Toro, western Uganda.

Range. Western Uganda and western Tanganyika Territory, west through Belgian Ruanda-Urundi to the Belgian Congo.

Genus **LACERTA** Linnaeus[79]

1758. **Lacerta* Linnaeus (part), Syst. Nat. ed. 10, **1**, p. 200. Type by designation of Fitzinger (1843:20): *L. agilis* Linnaeus.

1830. **Zootoca* Wagler, Nat. Syst. Amphib., p. 155. Type by designation of Fitzinger (1843:20): *Lacerta crocea* Wolf = *L. vivipara* Jacques.

1830. **Podarcis* Wagler (part), Nat. Syst. Amphib., p. 155. Type by designation of Fitzinger (1843:20): *Seps muralis* Laurenti.

1836. *Timon* Tschudi, Isis von Oken, **29**, p. 551. Type by original designation: *Lacerta ocellata* Daudin.

1838. *Teira* Gray, Ann. Nat. Hist., **1**, p. 280. Type by monotypy: *T. punctata* Gray = *Lacerta dugesii* Edwards.

1843. **Scelarcis* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta perspicillata* Duméril & Bibron.

1843. *Alsodromus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta maderensis* Fitzinger (*nomen nudum*).

1843. **Elaphropus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta galloti* Duméril & Bibron.

1843. *Chrysolamprus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta ocellata* Daudin.

1843. *Phenax* Fitzinger, Syst. Rept., p. 20. Type by original designation *Lacerta taurica* Pallas.

1845. *Thetia* Gray, Cat. Lizards Brit. Mus., p. 32. Type by monotypy: *Lacerta perspicillata* Duméril & Bibron.

1851. *Atropis* Gluckselig, Lotos, p. 138. Type by monotypy: *Lacerta nigra* Wolf = a melanistic mutation of *Lacerta vivipara* Jacques.

1868. *Agetosaura* Gistel, in Blicke, Leben Natur Menschen (Leipzig), p. 146. Type (*fide* Mertens:1936): *Lacerta margaritata* Schinz.

1868. *Thalestris* Gistel (not Claus:1863), in Blicke, Leben Natur

[79] Six of these names indicated by asterisks and here regarded as subgenera, were treated as "Sections" by Boulenger (1920, Monogr. Lacertidae, **1**, p. 37) though, as he ignored Fitzinger's names, he used *Thetia* (instead of *Scelarcis*) and proposed *Galiotia* (instead of *Elaphropus*). The only East African species, *L. jacksoni* Boulenger, he refers to *Podarcis*, while *vaucreselli* Tornier (which he had not seen) was assigned to *Zootoca*. I have since shown that it is an *Algyroides*, though with affinities to *jacksoni* that makes one wonder whether they are not congeneric.

Menschen (Leipzig), p. 148. Type (*fide* Mertens:1936): *Lacerta nigra* Wolf.

1868. *Tritonopsis* Gistel (not Conrad:1865), in Blicke, Leben Natur Menschen (Leipzig), p. 148. Type (*fide* Mertens:1936), the same as for *Thalestris*.

1916. *Gallotia* Boulenger, Trans. Zool. Soc. London, **21**, p. 3. Type by tautonomy: *Lacerta galloti* Duméril & Bibron.

1916. **Centromastix* Boulenger, Trans. Zool. Soc. London, **21**, p. 3. Type by monotypy: *Lacerta echinata* Cope.

Lacerta jacksoni Boulenger Jackson's Lizard

1899. *Lacerta jacksoni* Boulenger, Proc. Zool. Soc. London, p. 96, pl. x: Ravine Station, Mau Mountains, Kenya Colony.

1907. *Lacerta jacksoni kibonotensis* Lönnberg, in Sjöstedt, Wiss. Ergeb. Schwed. Zool. Exped. Kilimanjaro, Meru umbeg. Massaisteppen, No. 4, p. 5: "Kibonoto," i.e. Kibongoto, Kilimanjaro, Tanganyika Territory.

Range. Uganda; Kenya Colony and Tanganyika Territory, west through Belgian Ruanda-Urundi to the Belgian Congo.

Genus **NUCRAS** Gray

1838. *Nucras* Gray, Ann. Nat. Hist., **1**, p. 280. Type by monotypy: *Lacerta lalandii* Milne-Edwards.

1843. *Heliophilus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta delalandii* (*sic*) Milne-Edwards.

1886. *Bettaia* Bedriaga, Abhand. Senckenberg. Ges., **14**, No. 2, p. 24. Type by monotypy: *Lacerta delalandii* (*sic*) Milne-Edwards.

Nucras boulengeri boulengeri Neumann[80]
Uganda Savanna-Lizard

1900. *Nucras boulengeri* O. Neumann, Ann. Mag. Nat. Hist., (7) **5**, p. 56: "Lubwa's," i.e. Luba's Village, Busoga, Uganda.

1907. *Nucras emini* Boulenger, Ann. Mag. Nat. Hist., (7) **19**, p. 488: southern shore of Lake Victoria, Tanganyika Territory.

1909. *Nucras ukerewensis* Bolkay, Archivum Zool. Budapest, **1**, p. 13,

[80] If, as I believe, *Nucras succinea* Boulenger (1917, Ann. S. Africa Mus., **13**, p. 195, footnote) was in Zanzibar copal (instead of Baltic amber as alleged), then that name should be added to the synonymy. However, the status of these synonyms needs clarification, for two color forms appear to be involved — the slender, rufous lizard frequenting laterite areas of Tanganyika where it is to be found on native paths, and a more robust, dark olive, multiocellate, northeastern race represented in the Museum of Comparative Zoology by a series from Lolta Plains (M.C.Z. 17985-9) to which the name *ukerewensis* Bolkay seems applicable. Why Bolkay's single subadult ♂ holotype should have been so named is not clear. I saw no sign of the species during my short stay on Ukerewe Island in 1930.

figs. 1-4: Shirati, east shore of Lake Victoria, Tanganyika Territory.

Range. Uganda (east bank of Nile), east to Kenya Colony (Eldama Ravine), south through Tanganyika Territory (except around Kilosa) to the Rovuma River.

Nucras boulengeri kilosae Loveridge Keeled Savanna-Lizard

1922. *Nucras kilosae* Loveridge, Proc. Zool. Soc. London, p. 314: Kilosa, Usagara, Tanganyika Territory.

Range. Country around Kilosa, east-central Tanganyika Territory.

Genus **LATASTIA** Bedriaga

1884. *Latastia* Bedriaga, Ann. Mus. Civ. Stor. Nat. Genova, **20,** p. 307. Type by present designation: *Lacerta samharica* Blanford = *L. longicaudata* Reuss.

1907. *Apáthya* Méhely, Pótfüz. Természz. Köslöny (Budapest), **85,** p. 26. Type by monotypy: *Lacerta cappadocica* Werner.

Latastia longicaudata revoili (Vaillant)[81]
Southern Long-tailed Lizard

1882. *Eremias revoili* Vaillant, Miss. Révoil Pays Çomal., Rept., p. 20, pl. iii, fig. 2: Somaliland.

1884. *Latastia doriai* Bedriaga, Ann. Civ. Stor. Nat. Genova, **20,** p. 313: "Rugdeia Sogheira (Adal)."

1884. ?*Latastia doriai* var. *martensi* Bedriaga, Ann. Mus. Civ. Stor. Nat. Genova, **20,** p. 316: Keren, Bogos, Eritrea.

Range. (Northern limits uncertain; apparently arid areas of) Eritrea, south through Ethiopia and Kenya Colony to Ugogo, central Tanganyika Territory.

Latastia johnstoni Boulenger Nyasaland Long-tailed Lizard

1907. *Latastia johnstoni* Boulenger, Ann. Mag. Nat. Hist., (7) **19,** p. 392: "Masuka," i.e. Masuku, and Nyika Plateaus, Nyasaland.[82]

1919. *Latastia kidwelli* Boulenger, Trans. Royal Soc. S. Africa, **5,** p. 39: Eldorado, Southern Rhodesia.

1942. *Latastia bredoi* de Witte, Bull. Mus. Royal Hist. Nat. Belgique, **18,** p. 1, figs. 1-2: Musosa, Tanganyika District, Belgian Congo.

[81] *L. doriai* appears to be intermediate between *L. l. longicaudata* (Reuss) and *revoili* (Vaillant); whether it is subspecifically recognizable is somewhat doubtful though Parker (1942, Bull. Mus. Comp. Zool., **91,** p. 69) inclines to think it may prove so. Geographically its position is far from clear and calls for more material from the general region.

[82] Possibly from the lower slopes under 4000 feet, *not* from the plateaus (cf. Loveridge, 1953, Bull. Mus. Comp. Zool., **110,** p. 229).

Range. Central Tanganyika Territory, south through Mozambique; Nyasaland and both Rhodesias to the eastern Belgian Congo.

Genus **EREMIAS** Wiegmann[83]

1834. **Eremias* Wiegmann, Herp. Mexicana, p. 9. Type by subsequent designation of Boulenger:1918: *Lacerta velox* Pallas.

1838. **Mesalina* Gray, Ann. Nat. Hist., **1**, p. 282. Type by monotypy: *M. lichtensteinii* Gray = *Lacerta rubropunctata* Lichtenstein.

1841. *Aspidorhinus* Eichwald, Fauna Caspio-Caucasia, p. 74. Type by monotypy: *A. gracilis* Eichwald = *Lacerta velox* Pallas.

1843. *Eremioscopus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta guttulata* Lichtenstein.

1843. **Heliobolus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta lugubris* A. Smith.

1843. *Pataeosaurus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Lacerta capensis* A. Smith (not Sparrman:1783).

1843. *Pediophylax* Fitzinger, Syst. Rept., p. 21. Type by original designation: *Eremias dorsalis* Duméril & Bibron = *Lacerta lugubris* A. Smith.

1843. *Choroscopus* Fitzinger, Syst. Rept., p. 21. Type by original designation: *Eremias lineo-ocellata* Duméril & Bibron.

1843. *Eudioptra* Fitzinger, Syst. Rept., p. 21. Type by original designation: *Lacerta undata* A. Smith.

1843. *Dioptroblepharis* Fitzinger, Syst. Rept., p. 21. Type by original designation: *Eremias pardalis* Duméril & Bibron (not of Lichtenstein) = *Lacerta guttulata* Lichtenstein.

1843. *Pedioplanis* Fitzinger, Syst. Rept., p. 21. Type by original designation: *Eremias burchelli* Duméril & Bibron.

1843. *Tachyscelis* Fitzinger, Syst. Rept., p. 21. Type by original designation: *Lacerta rubropunctata* Lichtenstein.

1883. **Pseuderemias* Boettger, Abhand. Senckenberg. Naturf. Ges. **13**, p. 118, footnote. Type by monotypy: *P. lineolata* "Ruppell" Boettger = *Acanthodactylus mucronatus* Blanford.

1885. *Boulengeria* Lataste, Ann. Mus. Civ. Stor. Nat. Genova, (2) **2**, p. 126. Type by subsequent designation of Boulenger (1918): *Acanthodactylus mucronatus* Blanford.

1918. *Lampreremias* Boulenger, Journ. Zool. Res., **3**, p. 2. Type by original designation: *Eremias nitida* Günther.

[83] Five of these names, indicated by asterisks, correspond to "Sections" in Boulenger (1921, Monogr. Lacertidae, **2**, pp. 227-231) though his *Lampreremias* is antedated by *Heliobolus* Fitzinger, whose names he ignored — and not without reason for seven of Fitzinger's names are synonymous with *Mesalina* Gray.

1918. **Tanieremias* Boulenger, Journ. Zool. Res., **3**, p. 2. Type by original designation: *Eremias guineensis* Boulenger.

1928. *Ommateremias* Lantz, Bull. Muzei Gruzii, Tiflis, **4**, p. 37. Type by original designation: *Lacerta arguta* Pallas.

Eremias neumanni Tornier Neumann's Sand-Lizard

1905. *Eremias neumanni* Tornier, Zool. Jahrb. Syst., **22**, p. 376: "Barssa" i.e. Brussa Valley, north of Lake Stephanie, Ethiopia.

Range. Ethiopia, south to Ngatana, Tana River, Kenya Colony.

Ermias spekii sextaeniata Stejneger
Northern Speke's Sand-Lizard

1893. *Eremias sextaeniata* Stejneger, Proc. U. S. Nat. Mus., **16**, p. 718: Tana River, Kenya Colony.

Range. Southern Sudan and northern Uganda, east to British Somaliland, south through Somalia to northern Kenya Colony.

Eremias spekii spekii Günther Southern Speke's Sand-Lizard

1872. *Eremias spekii* Günther, Ann. Mag. Nat. Hist., (4) **9**, p. 381: Unyamwezi, Tanganyika Territory.

1878. *Eremias rugiceps* Peters, Monatsb. Akad. Wiss. Berlin, p. 202, pl. ii, fig. 1: "Taita," i.e. Teita, Kenya Colony.

Range. Kenya Colony (south of Tana River), south to central Tanganyika Territory.

Eremias smithi Boulenger Smith's Sand-Lizard

1895. *Eremias smithi* Boulenger, Proc. Zool. Soc. London, p. 534, pl. xxix, fig. 4: Milmil, in Haud, Ethiopia.

Range. Ethiopia and British Somaliland, south through Somalia to the Tana River, Kenya Colony.

Eremias striata Peters Peter's Sand-Lizard

1874. *Eremias brenneri* var. *striatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 370: "Barawa," i.e. Brava, Somalia.

1893. *Eremias hoehnelı* Stejneger, Proc. U. S. Nat. Mus., **16**, p. 719: Tana River, Kenya Colony.

Range. British Somaliland, south through Somalia to the Tana River, Kenya Colony.

Genus **ICHNOTROPIS** Peters

1843. *Thermophilus* Fitzinger (not *Thermophila* Hübner:1816), Syst. Rept., p. 21. Type by original designation: *Tropidosaura capensis* Duméril & Bibron = *Algyra capensis* A. Smith.

1854. *Ichnotropis* Peters, Monatsb. Akad. Wiss. Berlin, p. 617. Type by subsequent designation: *I. macrolepidota* Peters = *Algyra capensis* A. Smith.

Ichnotropis tanganicana Boulenger

Tanganyika Rough-scaled Sand-Lizard

1917. *Ichnotropis tanganicana* Boulenger, Ann. Mag. Nat. Hist., (8) **19**, p. 278: East coast of Lake Tanganyika, Tanganyika Territory.

Range. Tanganyika Territory (known only from the holotype).

Ichnotropis capensis bivittata Bocage

Angola Rough-scaled Sand-Lizard

1866. *Ichnotropis bivittata* Bocage, Jorn. Sci. Lisboa, **1**, p. 43: Duque de Braganca, Angola.

Range. Southern Tanganyika Territory, west through Belgian Congo to Angola, possibly north to French Congo.

Ichnotropis squamulosa Peters

Mozambique Rough-scaled Sand-Lizard

1854. *Ichnotropis squamulosa* Peters, Monatsb. Akad. Wiss. Berlin, p. 617: Tete, Mozambique.

Range. Tanganyika Territory, south through Mozambique to Zululand, Natal, west through Transvaal and Bechuanaland to Southwest Africa, north to Angola.

Family VARANIDAE

Genus **VARANUS** Merrem[84]

1818. *Monitor* Lichtenstein (not Blainville:1816), Zool. Mus. Univ. Berlin (2), p. 66. Type by tautonomy: *Lacerta monitor* Linnaeus (part) = *L. nilotica* Linnaeus (part).

1820. **Varanus* Merrem, Vers. Syst. Amphib., pp. 13, 58. Type by subsequent designation: *Lacerta varia* Shaw.

1826. **Psammosaurus* Fitzinger, Neue Class. Rept., pp. 21, 50. Type by monotypy: *Tupinambis griseus* Daudin.

1827. *Uaranus* Gray, Philos. Mag., (n.s.) **2**, p. 55. Emendation of *Varanus* Merrem.

1827. *Dracaena* Gray (not Daudin:1802), Philos. Mag., (n.s.) **2**, p. 55.

[84] Eight of these names, indicated by asterisks, are valid subgenera according to Mertens (1942, Abhand. Senckenberg. Naturf. Ges., No. 466, p. 242: key) whose comprehensive and careful revision of the VARANIDAE has been of the greatest help.

Type by tautonomy: *Lacerta dracaena* Linnaeus = *Tupinambis bengalensis* Daudin.

1830. *Hydrosaurus* Wagler (not Kaup:1828), Nat. Syst. Amphib., pp. 132, 164. Type by subsequent designation: *Tupinambis bivittatus* Kuhl = *Stellio salvator* Laurenti.

1830. **Polydaedalus* Wagler, Nat. Syst. Amphib., pp. 132, 164. Type by subsequent designation: *Lacerta nilotica* Linnaeus.

1838. **Empagusia* Gray, Ann. Nat. Hist., **1**, p. 393. Type by subsequent designation: *Monitor flavescens* Hardwicke & Gray.

1838. **Odatria* Gray, Ann. Nat. Hist., **1**, p. 394. Type by monotypy: *O. punctata* Gray = *Monitor tristis* Schlegel.

1843. *Cylindrurus* Fitzinger, Syst. Rept., p. 19. Type by original designation. *Odatria punctata* Gray = *Monitor tristis* Schlegel.

1843. *Panthcrosaurus* Fitzinger, Syst. Rept., p. 19. Type by original designation: *Hydrosaurus gouldii* Gray.

1843. *Agalmatosaurus* Fitzinger, Syst. Rept., p. 19. Type by original designation: *Monitor timorensis* Gray.

1843. *Euprepiosaurus* Fitzinger, Syst. Rept., p. 19. Type by original designation: *Varanus chlorostigma* Duméril & Bibron = *Tupinambis indicus* Daudin.

1843. *Pachysaurus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Tupinambis albigularis* Daudin.

1843. *Rhinoptyon* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Varanus ocellatus* Rüppell = *Lacerta exanthematica* Bosc.

1843. *Psammoscopus* Fitzinger, Syst. Rept., p. 20. Type by original designation: *Varanus picquotii* Duméril & Bibron = *Monitor flavescens* Hardwicke & Gray.

1845. *Regenia* Gray, Cat. Lizards Brit. Mus., p. 8. Type by subsequent designation: *Tupinambis albigularis* Daudin.

1927. *Placovaranus* Fejervary, Természettudomanyi Közlöny, **59**, p. 284. Type by original designation: *Varanus komodoensis* Ouwens.

1942. **Indovaranus* Mertens, Abhand. Senckenberg. Naturf. Ges., No. 466, p. 240. Type by original designation: *Tupinambis bengalensis* Daudin.

1942. **Dendrovaranus* Mertens, Abhand. Senckenberg. Naturf. Ges., No. 466, p. 241. Type by original designation: *Uaranus rudicollis* Gray.

1942. **Tectovaranus* Mertens, Abhand. Senckenberg. Naturf. Ges., No. 466, p. 242. Type by original designation: *Monitor dumerili* Schlegel.

Varanus niloticus niloticus (Linnaeus) Nile Monitor

1758. *Lacerta monitor* Linnaeus (part), Syst. Nat., ed. 10, **1**, p. 201: "in Indiis," i.e. Africa.

1766. *Lacerta nilotica* Linnaeus, Syst. Nat., ed. 12, **1**, p. 369: Egypt.

1768. *Stellio saurus* Laurenti, Syn. Rept., p. 56: "in Zeylania ad littora maris."

1783. *Lacerta capensis* Sparrman, Resa till Goda Hoppsudden, p. 749: "Hinterbruyntjes Heights," = Bruintjeshoogte, a village between Pearston and Somerset East, eastern Cape Province.[85]

1788. "*L. tupinambis*" Lacépède (part),[86] Hist. Nat. Quad. ovip. Serpens, **1**, Synopsis Methodica, p. 251, pl. xvii: restricted to Cape of Good Hope, i.e. South Africa.

1802. *Tupinambis elegans* Daudin (part), Hist. Nat. Rept., **3**, p. 36: "Amerique méridionale" (error).

1802. *Tupinambis stellatus* Daudin, Hist. Nat. Rept., **3**, p. 59, pl. xxxi: Senegal (restricted).

1819. *Monitor pulcher* Leach, in Bowdich, Miss. Ashantee, App., p. 493: "Fantee," i.e. Fanti, Ashanti, Gold Coast.

1844. *Monitor elegans senegalensis* Schlegel, Abbild. Amphib., p. x: Senegal.

Range. Africa (exclusive of arid areas in the north and southwest, also the rain-forest region of the west[87]), including Uganda; Kenya Colony; Tanganyika Territory; Zanzibar and Mafia Islands.

Varanus exanthematicus microstictus Boettger[88]

Eastern Savanna-Monitor

1845. *Monitor microstictus* Rüppell (*nomen nudum*), Mus. Senckenberg., **3**, p. 301: "Abyssinien," i.e. Ethiopia.

1893. *Varanus microstictus* Boettger, Kat. Rept. Samml. Mus. Senckenberg. Naturf. Ges., Part 1, pp. viii, 72: Ethiopia.

Range. Ethiopia and British Somaliland, south through Uganda; Kenya Colony; Tanganyika Territory and Zanzibar Island to Mozambique (where it meets with the southern race, *V. e. albigularis* (Daudin)).

[85] Dr. V. F. FitzSimons, to whom I am indebted for the above information, informs me that this locality appears on Sparrman's map (1876) as "Agterbruntjes Hoogte."

[86] Only the vernacular name is given, not *"Lacertus tupinambis"* as cited by some authors. In fact it is listed with the crocodilians in the Synopsis Methodica.

[87] The only race, *V. n. ornatus* (Daudin), has a *discontinuous* distribution in the surviving patches of rain forest from the western Belgian Congo and Cameroons to Liberia. The species is referable to the subgenus *Polydaedalus*.

[88] This is the monitor which for a century has been miscalled *Varanus ocellatus* (Heyden in Rüppell), a name that is actually synonymous with *V. e. exanthematicus* (Bosc) which ranges from Eritrea to Senegal.

Family AMPHISBAENIDAE

Genus **ANCYCLOCRANIUM** Parker

1942. *Ancyclocranium* Parker, Bull. Mus. Comp. Zool., **91**, p. 37: Type by original designation: *Anops somalicus* Scortecci.

Ancyclocranium barkeri Loveridge

Lindi Sharp-snouted Worm-Lizard

1942. *Ancyclocranium barkeri* Loveridge, Proc. Biol. Soc. Washington, **59**, p. 73, pl. xiii: Mbemkuru River, Lindi district, Tanganyika Territory.

Range. Tanganyika Territory (known only from holotype).

Ancyclocranium ionidesi Loveridge

Kilwa Sharp-snouted Worm-Lizard

1955. *Ancylocranium ionidesi* Loveridge, Journ. E. Africa Nat. Hist. Soc., **22**, p. 177, pl. —: Kilwa, Southern Province, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type series).

Genus **AMPHISBAENA** Linnaeus[89]

1758. **Amphisbaena* Linnaeus, Syst. Nat. ed. 10, **1**, p. 229. Type by subsequent designation: *A. fuliginosa* Linnaeus.

1844. *Sarea* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 71. Type by monotypy: *Amphisbaena caeca* Cuvier.

1844. **Cynisca* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 71. Type by monotypy: *Amphisbaena leucura* Duméril & Bibron.

1861. **Diphalus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 75. Type by original designation: *D. fenestratus* Cope.

1865. **Bronia* Gray, Proc. Zool. Soc. London, p. 448. Type by monotypy: *B. brasiliana* Gray.

1878. *Ophioproctes* Boulenger, Bull. Soc. Zool. France, **3**, p. 300. Type by monotypy: *O. liberiensis* Boulenger.

1885. *Aporarchus* Cope, Proc. American Philos. Soc., **22**, p. 187. Type by monotypy: *Amphisbaena prunicolor* Cope.

1885. *Zygnis* Cope (not Oken:1816), Proc. American Philos. Soc., **22**, p. 188. Type by monotypy: *Amphisbaena quadrifrons* Peters.

1907. **Chirindia* Boulenger, Ann. Mag. Nat. Hist., (7) **20**, p. 48. Type by monotypy: *C. swynnertoni* Boulenger.

[89] Seven of these names, indicated by asterisks, here regarded as subgenera, are considered full genera by Vanzolini (1951, Herpetologica, **7**, pp. 113-123). Five of the six East African species would be assigned to as many different subgenera, with his *Shrevea* replacing *Zygnis* Cope (preoccupied).

1911. *Amphisbaenula* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 246. Type by monotypy: *A. orientalis* Sternfeld.

1951. **Loveridgea* Vanzolini, Herpetologica, **7**, p. 114. Type by original designation: *Amphisbaena phylofiniens* Tornier.

1951. **Shrevea* Vanzolini, Herpetologica, **7**, p. 115. Type by original designation: *Amphisbaena quadrifrons* Peters.

Amphisbaena ionidesii Battersby Liwale Worm-Lizard

1950. *Amphisbaena ionidesii* Battersby, Ann. Mag. Nat. Hist., (12) **3**, p. 413, fig. —: Liwale, Southern Province, Tanganyika Territory.

Range. Tanganyika Territory.

Amphisbaena phylofiniens Tornier Ujiji Worm-Lizard

1899. *Amphisbaena phylofiniens* Tornier, Zool. Anz., **22**, p. 260: Ujiji, Tanganyika Territory.

Range. Tanganyika Territory.[90]

Amphisbaena mpwapwaensis Loveridge
Mpwapwa Worm-Lizard

1932. *Amphisbaena mpwapwaensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 378: Mpwapwa, Ugogo, Tanganyika Territory.

Range. Tanganyika Territory.[90]

Amphisbaena ewerbecki (Werner) Mbanja Worm-Lizard

1910. *Chirindia ewerbecki* Werner, 1909, Jahrb. Hamburg, Wiss. Anst., **27**, p. 37: Mbanja near Lindi, Tanganyika Territory.

Range. Tanganyika Territory.[90]

Amphisbaena rondoensis Loveridge Nchingidi Worm-Lizard

1941. *Amphisbaena rondoensis* Loveridge, Bull. Mus. Comp. Zool., **87**, p. 394, fig. 23: Nchingidi, Rondo Plateau, Lindi district, Tanganyika Territory.

Range. Tanganyika Territory.[90]

Amphisbaena orientalis (Sternfeld) Mikindani Worm-Lizard

1911. *Amphisbaenula orientalis* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 246: Mikindani, Southern Province, Tanganyika Territory.

Range. Tanganyika Territory.[90]

Genus **GEOCALAMUS** Günther

1880. *Geocalamus* Günther, Ann. Mag. Nat. Hist., (5) **6**, p. 234. Type by monotypy: *G. modestus* Günther.

[90] Only from vicinity of the type locality.

Geocalamus acutus Sternfeld

Voi Wedge-snouted Worm-Lizard

1912. *Geocalamus acutus* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 209: Voi, Kenya Colony.

1913. *Geocalamus noltei* Boettger, in Voeltzkow, Reise in Ostafrika, **3**, p. 366, pl. xxvi, fig. 6: Moshi, Tanganyika Territory.

Range. Kenya Colony and Tanganyika Terirtory.

Geocalamus modestus Günther

Mpwapwa Wedge-snouted Worm-Lizard

1880. *Geocalamus modestus* Günther, Ann. Mag. Nat. Hist., (5) **6**, p. 234: Mpwapwa, Ugogo, Tanganyika Territory.

Range. Tanganyika Territory.

Suborder SERPENTES [91]

Family TYPHLOPIDAE

Genus **TYPHLOPS** Oppel[92]

1811. *Typhlops* Oppel, Ordn. Fam. Gattung Rept., p. 54. Type by subsequent designation: *Anguis lumbricalis* Linnaeus.

1830. *Typhlina* Wagler (not *Typhline* Wiegmann), Nat. Syst. Amphib., p. 196. Type by subsequent designation: "*Acontias lineatus* Reinw." = *Typhlops lineatus* Boie.[93]

1843. *Aspidorhynchus* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Typhlops eschriehtii* Schelegel = *Acontias punctatus* Leach.

1843. *Gerrhopilus* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Typhlops ater* Schlegel.

1843. *Pseudotyphlops* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Typhlops polygrammicus* Schlegel.

1843. *Rhinotyphlops* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Typhlops lalandii* Schlegel.

1843. *Ramphotyphlops* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Typhlops multilineatus* Schlegel.

[91] OPHIDIA of Macartney (1802), Boulenger (1893) and others.

[92] Oppel ascribes the name to Schneider, but Schneider (1801) used Typhlopes in a plural sense of family proportions. Oppel, by his inclusion of *striatus*, apparently regarded *Typhlops* as a masculine noun to which adjectival endings should conform. Despite Oppel's views some scholars are confident it is feminine. however, I have hesitated to make any changes.

[93] In case Fitzinger's (1843) designation or later ones be considered inadequate, the type of *Typhlina* is hereby fixed as above to avoid any possibility of *Typhlops septemstriatus* Schneider being selected, for this would affect the use of *Leptotyphlops* and LEPTOTYPHLOPIDAE.

1844. *Pilidion* Duméril & Bibron, Erpét. Gén., **6**, p. 257. New name for *Typhlina lineatus* Wagler = *Typhlops lineatus* Boie.

1844. *Ophthalmidium* Duméril & Bibron, Erpét. Gén., **6**, p. 262. Type by subsequent designation: *O. longissimum* Duméril & Bibron.

1844. *Cathetorhinus* Duméril & Bibron, Erpét. Gén., **6**, p. 268. Type by monotypy: *C. melanocephalus* Duméril & Bibron.

1844. *Onychocephalus* Duméril & Bibron, Erpét. Gén., **6**, p. 272. Type by subsequent designation: *Typhlops lalandii* Schlegel.

1845. *Onychophis* Gray, Cat. Lizards Brit. Mus., p. 132. Type by monotypy: *O. franklinii* Gray = *Typhlops lalandii* Schlegel.

1845. *Typhlinalis* Gray, Cat. Lizards Brit. Mus., p. 134. New name for *Typhlina* Wagler.

1845. *Anilios* Gray, Cat. Lizards Brit. Mus., p. 135. Type by present designation: *A. leachii* Gray = *Anguis lumbricalis* Linnaeus.

1845. *Argyrophis* Gray, Cat. Lizards Brit. Mus., p. 136. Type by present designation: *A. bicolor* Gray = *Typhlops nigroalbus* Duméril & Bibron.

1845. *Meditoria* Gray, Cat. Lizards Brit. Mus., p. 139. Type by monotypy: *M. nasuta* Gray = *Anguis lumbricalis* Linnaeus.

1861. *Diaphorotyphlops* Jan, Arch. Zool. Anat. Fisiol., **1**, p. 185. Type by subsequent designation: *D. disparilis* Jan.

1868. *Letheobia* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 322. Type by designation of Dunn & Dunn (1940: Copeia, p. 75): *L. pallida* Cope.

1881. *Grypotyphlops* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 70. Type by original designation: *Onychocephalus acutus* Duméril & Bibron.

Typhlops blanfordii blanfordii Boulenger

Ethiopian Blind-Snake

1889. *Typhlops Blanfordii* Boulenger, Ann. Mag. Nat. Hist., (6) **4**, p. 363: Senafe, Ethiopia.

Range. Eritrea and Ethiopia, south to northern Kenya Colony (at Moyale; *fide* Scortecci:1940).

Typhlops blanfordii lestradei Witte[94] Ruanda Blind-Snake

1933. *Typhlops Lestradei* de Witte, Revue Zool. Bot. Afr., **23**, p. 206, figs. 1-3: "Rubengera" *i.e.* Ruhengeri, Belgian Ruanda-Urundi.

Range. Uganda, west through Belgian Ruanda-Urundi to Belgian Congo.

Typhlops schlegelii brevis Scortecci

Northern Schlegel's Blind-Snake

[94] For detailed discussion of relationships with *adolfi* Sternfeld and *dubius* Chabanaud, see Loveridge, 1942, Bull. Mus. Comp. Zool., **91**, pp. 254-255, pl. ii, fig. 2.

1929. *Typhlops brevis* Scortecci, Atti Soc. Ital. Sci. Nat. (Milano), **68**, p. 287: Chisimaio (Kismayu), Somalia.

Range. Southern Sudan and Uganda (Lado Enclave); British Somaliland south through Somalia (probably to northern Kenya Colony).

Typhlops schlegelii excentricus Procter
Dark-bellied Blind-Snake

1922. *Typhlops excentricus* Procter, Ann. Mag. Nat. Hist., (9) **9**, p. 685: Kilosa, Tanganyika Territory.

Range. Tanganyika Territory (an east-central area from Mpwapwa to Morogoro).

Typhlops schlegelii mucruso (Peters)[95]
Eastern Schlegel's Blind-Snake

1854. *Onychocephalus mucruso* Peters (part), Monatsb. Akad. Wiss. Berlin, p. 621: Macanga, Mozambique.

1873. *Onychocephalus Petersii* Bocage, Jorn. Sci. Lisboa, **4**, p. 249: Bibala, Mossamedes, Angola.

1886. *Typhlops* (*Onychocephalus*) *humbo* Bocage, Jorn. Sci. Lisboa, **11**, p. 171: Quisange, Benguela, Angola.

1893. *Typhlops hottentotus* Bocage, Jorn. Sci. Lisboa, (2) **3**, p. 117: Quindumbo, Benguela, Angola.

1893. *Typhlops mandensis* Stejneger, Proc. U. S. Nat. Mus., **16**, p. 725: Wange, mainland *opposite* Manda Island, Kenya Colony.

1910. *Typhlops latirostris* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 70: Tabora, Tanganyika Territory.

1912. *Typhlops viridiflavus* Peracca, Ann. Mus. Zool. Univ. Napoli, (2) **3**, No. 25, p. 3: Lake Bangweulu, Northern Rhodesia.

Range. Kenya Colony; Tanganyika Territory and Zanzibar Island, south to Mozambique north of the Zambezi River,[96] west through Nyasaland and Northern Rhodesia to Angola.

Typhlops punctatus punctatus (Leach)[97] Spotted Blind-Snake

1819. *Acontias punctatus* Leach, in Bowdich, Miss. Ashantee, App., p. 493: "Fantee," i.e. Fanti, Ashanti, Gold Coast.

1844. *Typhlops eschrichtii* Schlegel, Abbild. Amphib., p. 37, pl. xxxii, figs. 13, 16: Gold Coast.

[95] Owing to young individuals having rounded snouts resembling those of *punctatus*, they have often been reported as that species. Direct comparison of the types of the numerous synonyms of both species is very much needed.

[96] An arbitrary boundary, for the two races merge in this vicinity. *T. s. schlegelii* (Peters) ranges over the whole of Africa south of the river.

[97] Several other forms, which should perhaps be added to this synonymy, have been described in the last thirty-five years.

1844. *Onychocephalus congestus* Duméril & Bibron, Erpét. Gén., **6**, p. 265: No locality.

1845. *Onychophis Barrowii* Gray, Cat. Lizards Brit. Mus., p. 133: "India?"

1848. *Onychocephalus Liberiensis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 59: Liberia.

1848. *Onychocephalus nigro-lineatus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 60: Liberia.

1864. *Typhlops liberiensis* var. *intermedia* Jan, Icon. Gén. Ophid., p. 24, and **1**, livr. 5, pls. v-vi, fig. 2: Liberia.

1864. *Typhlops Kraussi* Jan, Icon. Gén. Ophid., p. 26, and **1**, livr. 3, pl. vi, fig. 2: Gold Coast.

1864. *Typhlops lincolatus* Jan, Icon. Gén. Ophid., p. 24, and **1**, livr. 9, pl. i, fig. 4: Sierra Leone.

1866. *Onychocephalus angolensis* Bocage, Jorn. Sci. Lisboa, **1**, p. 46: Duque de Braganca, Angola.

1887. *Typhlops* (*Onychocephalus*) *congicus* Boettger, Zool. Anz., **10**, p. 650: Povo Netonna, near Banana, Belgian Congo.

1893. *Typhlops boulengeri* Bocage, Jorn. Sci. Lisboa, (2) **3**, p. 117: Interior of Benguela, Angola.

1904. *Typhlops bocagei* Ferreira, Joru. Sci. Lisboa, (2) **7**, p. 114: Cabicula, Bom Jesus, Angola.

1910. *Typhlops Tornieri* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 69: Mount Kilimanjaro, Tanganyika Territory.

1910. *Typhlops Adolphi* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 70: "Fort Blus," later corrected to Fort Beni, Belgian Congo.

1917. *Typhlops dubius* Chabanaud, Bull. Mus. Hist. Nat. (Paris), 1916, **22**, p. 364: "Kivori," i.e. Kivu Volcanoes, 1500 metres, Belgian Congo.

1920. *Typhlops Milleti* Chabanaud, Bull. Mus. Hist. Nat. (Paris), **26**, p. 463: Togo.

Range. Forested areas of Uganda; montane forests of Kenya Colony and Tanganyika Territory, southwest to Angola and northwest to Senegal (frequently recorded in error for other species).

Typhlops punctatus gierrai Mocquard

Usambara Spotted Blind-Snake

1897. *Typhlops Gierrai* Mocquard, Bull. Mus. Hist. Nat. (Paris), **3**, p. 122: Tanga, Tanganyika Territory.

Range. Virgin forests of the Usambara and Uluguru Mountains (possibly the gallery forests of adjacent lowlands also), Tanganyika Territory.

Typhlops kaimosae Loveridge Kakamega Spotted Blind-Snake

1935. *Typhlops kaimosae* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 5: Kaimosi, Kakamega, Nyanza Province, Kenya Colony.

Range. Kenya Colony (known only from the holotype; possibly an aberrant *punctatus* in which the preocular is separated from the upper labials by nasal and ocular).

Typhlops tettensis tettensis (Peters) Tete Blind-Snake

1860. *Onychocephalus tettensis* Peters, Monatsb. Akad. Wiss. Berlin, p. 80: Tete, Mozambique.

Range. Kilwa and Liwale, Tanganyika Territory, southwest to Tete, Mozambique.

Typhlops tettensis rondoensis Loveridge Rondo Blind-Snake

1942. *Typhlops tettensis rondoensis* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 256: Nchingidi, Rondo Plateau, Lindi district, Tanganyika Territory.

Range. Rondo Plateau, Tanganyika Territory.

Typhlops unitaeniatus unitaeniatus Peters
Stripe-backed Blind-Snake

1878. *Typhlops (Letheobia) unitaeniatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 205, pl. ii, fig. 5: "Taita," i.e. Teita, Kenya Colony.

Range. Somalia (where the race *ataeniatus* Boulenger also occurs), south through coastal Kenya Colony to Buhuri, northeast Tanganyika Territory.

Typhlops platyrhynchus Sternfeld Tanga Blind-Snake[98]

1910. *Typhlops platyrhynchus* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 69: Tanga, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type locality).

Typhlops graueri Sternfeld Lake Tanganyika Blind-Snake

1912. *Typhlops graueri* Sternfeld, Wiss. Ergebn. Deutsch. Zentral-Afrika-Exped. 1907-1908, **4**, p. 264: Virgin forest behind boundary mountains on northwest of Lake Tanganyika, Belgian Congo.

Range. Ujiji, Tanganyika Territory, northwest to Medje, Belgian Congo.

Typhlops gracilis Sternfeld Urungu Blind-Snake

1910. *Typhlops gracilis* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 70: Kitungulu, Urungu, Tanganyika Territory.

[98] *Typhlops opisthopachys* Werner (1917), allegedly from Tanga, has been shown by me to be a synonym of the Australian *pinguis* Waite.

Range. Southwestern Tanganyika Territory and Northern Rhodesia.

Typhlops pallidus (Cope) Zanzibar Blind-Snake

1868. *Letheobia pallida* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 322: Zanzibar Island.

Range. Southern Sudan; coastal belt of Kenya Colony and Tanganyika Territory; Pemba and Zanzibar Islands.

Typhlops uluguruensis Barbour & Loveridge
Uluguru Blind-Snake

1928. *Typhlops uluguruensis* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 104: Nyange, Uluguru Mountains, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type locality).

Typhlops braminus (Daudin)
Brahminy or Flower-Pot Blind-Snake

1803. *Eryx braminus* Daudin, Hist. Nat. Rept., **7**, p. 279: Bengal, India.
1820. *Tortrix Russellii* Merrem, Vers. Syst. Amphib., p. 85: India orientali.
1838. *Onychocephalus Capensis* A. Smith, Illus. Zool. S. Africa, Rept., pl. ii, fig. 3; pl. liv, figs. 9-16: South Africa ("Interior of" may be considered to be erroneous).
1845. *Argyrophis truncatus* Gray, Cat. Lizards Brit. Mus., p. 138: Philippine Islands.
1860. *Ophthalmidium tenue* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 497 (type believed lost): Hong Kong.
1863. *Typhlops inconspicuous* Jan, Elenco Sist. Degli Ofidi, p. 11: Madagascar.
1864. *Typhlops pammeces* Günther (new name for *tenue* Hallowell: preoccupied), Rept. British India, p. 176, pl. xvi, fig. C.
1882. *Typhlops* (*Typhlops*) *euproctus* Boettger, Zool. Anz., **5**, p. 479: Loucoubé, Nossi Bé, Madagascar.
1889. *Typhlops comorensis* Boulenger, Ann. Mag. Nat. Hist., (6) **4**, p. 361: Comoro Islands.
1906. *Typhlops braminus* var. *arenicola* Annandale, Mem. Asiatic Soc. Bengal, **1**, p. 192: Ramnad, South India.
1906. *Typhlops limbricki* Annandale, Mem. Asiatic Soc. Bengal, **1**, p. 193: Ramnad, South India.
1909. *Typhlops braminus* var. *pallidus* Wall (not Cope:1868), Journ. Bombay Nat. Hist. Soc., **19**, p. 609: Dibrugarh, Upper Assam.
1909. *Typhlops microcephalus* Werner, Jahresb. Ver. Nat. Württemberg

(Stuttgart), **65**, p. 60: Madagascar.

1910. *Glauconia braueri* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 69: Bagamoyo, Tanganyika Territory.

1918. *Typhlops capensis* Rendahl (sp. n.; not of A. Smith), Arkiv. Zool., **11**, No. 17, p. 1, figs. 1-3: "Capeland," i.e. South Africa.

1919. *Typhlops fletcheri* Wall, Journ. Bombay Nat. Hist. Soc., **26**, p. 556: Nilgiris, India.

Range. Coastal zone of Kenya Colony; Tanganyika Territory; Mozambique and South Africa. On islands of Socotra; Zanzibar; Comoro; Madagascar and Mauritius.[99]

Southern Europe and Asia (Arabia to China); islands of the Indian Ocean; China Sea; Pacific Ocean (Marianna; Caroline; Marshall; Solomon; Hawaiian); West Indies; South America (Mexico to Argentina).

Typhlops lumbriciformis (Peters) Wormlike Blind-Snake

1874. *Onychocephalus* (*Letheobia*) *lumbriciformis* Peters, Monatsb. Akad. Wiss. Berlin, p. 377: "Zanzibar Coast," i.e. Tanganyika Territory.

1904. *Typhlops kleebergi* Werner, Zool. Anz., **27**, p. 464: Usambara, Tanganyika Territory.

Range. Coastal Kenya Colony and Tanganyika Territory; Zanzibar Island.[100]

Family LEPTOTYPHLOPIDAE

Genus **LEPTOTYPHLOPS** Fitzinger

1824. *Stenostoma* Wagler (not Latreille:1810), in Spix, Serp. Brasil., p. 68. Type by monotypy: *S. albifrons* Wagler.

1843. *Leptotyphlops* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Typhlops nigricans* Schlegel.

1843. *Eucephalus* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Typhlops bilineatus* Schlegel.

[99] The world-wide distribution of this tiny snake is attributable to transport in soil surrounding the roots of introduced plants, at other times in ballast. Its first appearance in a country is apt to lead to redescription. The above list of synonyms is not necessarily complete. Possibly some of the five *Typhlops* with 20 midbody scale-rows, described from Ceylon by Taylor (1947, Univ. Kansas Sci. Bull., **31**, pp. 287-298) may be based on individual variants. The Malagasy species *reuteri* Boettger (1882), together with its synonym *lenzi* Boettger (1882), was removed from the synonymy by Mertens in 1922.

[100] The snake from "Fwambo," i.e. Fwamba, Northern Rhodesia, assigned to *lumbriciformis* by Boulenger (1896, Cat. Snakes Brit. Mus., **3**, p. 590), is actually referable to *T. gracilis* Sternfeld (1910) which occurs at nearby Abercorn.

1844. *Catodon* Duméril & Bibron (not Linnaeus:1761), Erpét. Gén., **6**, p. 318. Type by monotypy: *Typhlops septemstriatus* Schneider.

1845. *Glauconia* Gray, Cat. Lizards Brit. Mus., p. 139. Type by monotypy: *Typhlops nigricans* Schlegel.

1845. *Epictia* Gray, Cat. Lizards Brit. Mus., p. 139. Type by present designation: *Typhlops undecimstriatus* Schlegel = *Stenostoma albifrons* Wagler.

1853. *Rena* Baird & Girard, Cat. N. American Rept., p. 142. Type by subsequent designation: *R. dulcis* Baird & Girard.

1857. *Sabrina* Girard, Proc. Acad. Nat. Sci. Philadelphia, p. 181. Type monotypy: *Typhlops tessellatum* Tschudi = *Stenostoma albifrons* Wagler.

1861. *Rhamphostoma* Jan (not Wagler:1830), Arch. Zool. Anat. Phys., **1**, p. 190: Type by monotypy: *Stenostoma macrorhynchum* Jan.

1861. *Tricheilostoma* Jan, Arch. Zool. Anat. Phys., **1**, p. 190. Type by present designation: *Stenostoma macrolepis* Peters.

1861. *Tetracheilostoma* Jan, Arch. Zool. Anat. Phys., **1**, p. 191. Type by monotypy: *Typhlops bilineatus* Schlegel.

1881. *Siagonodon* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 71. Type by original designation: *Typhlops septemstriatus* Schneider.

1885. *Stenostomophis* Rochebrune, Faune Senegambie, Rept., p. 142. New name for *Stenostoma* Wagler (preoccupied).

Leptotyphlops conjuncta conjuncta (Jan)[101]

Jan's All-black Worm-Snake

1861. *Stenostoma conjunctum* Jan, Arch. Zool. Anat. Fisiol., **1**, p. 189: South Africa.

1876. *Stenostoma groutii* Cope, Journ. Acad. Nat. Sci. Philadelphia, (2) **8**, p. 128: Umvoti Mission, Natal.

1909. *Glauconia merkeri* Werner, Jahres. Ver. Nat. Württemberg, **65**, p. 61: Moshi, Tanganyika Territory.

1912. *Glauconia latirostris* Sternfeld, Wiss. Ergebn. Deutsch. Zentral-Afrika-Exped. 1907-1908, **4**, p. 264: Northwest of Lake Tanganyika Territory, Belgian Congo.

Range. Uganda (Entebbe); Kenya Colony and Tanganyika Territory south to Natal.[102]

Leptotyphlops boulengeri (Boettger)

Manda Flesh-pink Worm-Snake

[101] Occasionally East African specimens have been identified as *distanti* (Boulenger); *nigricans* (Schlegel); *scutifrons* (Peters) or *signata* (Jan).

[102] In Transvaal this form meets with the western race *L. c. distant* (Boulenger) of Southern Rhodesia and Bechuanaland.

1913. *Glauconia boulengeri* Boettger, in Voeltzkow, Reise in Ost-afrika, **3**, p. 354, pl. xxv, fig. 1: Manda Island, Kenya Colony.

Range. Manda and Lamu Islands, Kenya Colony.

Leptotyphlops emini emini (Boulenger)[103]
Emin's All-black Worm-Snake

1890. *Glauconia emini* Boulenger, Ann. Mag. Nat. Hist., (6) **6**, p. 91: Karagwe [district, Bukoba, Tanganyika Territory].

Range. (Ethiopia and Somalia); southern Sudan; Uganda; Kenya Colony; Tanganyika Territory (and Mafia Island), west through Belgian Ruanda-Urundi and eastern Belgian Congo to Nyamkolo, Northern Rhodesia.

Leptotyphlops emini pembae Loveridge
Pemba White-chinned Worm-Snake

1941. *Leptotyphlops emini pembae* Loveridge, Proc. Biol. Soc. Washington, **54**, p. 177: Wingwi Pwana, Pemba Island.

Range. Pemba Island (abundant).

Leptotyphlops longicauda (Peters)
Long-tailed Flesh-pink Worm-Snake

1854. *Stenostoma longicaudum* Peters, Monatsb. Akad. Wiss. Berlin, p. 621: Tete, Mozambique.

Range. [104]Coastal Kenya Colony; Tanganyika Territory and Mozambique, east through Nyasaland to Northern Rhodesia.

Leptotyphlops fiechteri (Scortecci) White-bellied Worm-Snake

1929. *Glauconia fiechteri* Scortecci, Atti. Soc. Ital. Sci. Nat. (Milano), **68**, p. 266, figs. —: Villaggio Duca degli Abruzzi, Somalia.

Range. Somalia, south to Lake Rudolf, Kenya Colony.

Family BOIDAE

Subfamily PYTHONINAE

Genus **PYTHON**[105] Daudin

[103] Ethiopian and Somali snakes have a white-tipped tail, so may be subspecifically distinguishable as suggested by Parker (1949).

[104] Reported, with a question mark as to identification, from Somalia by Scortecci (1939).

[105] *Morelia* Gray (1842) is regarded as generically distinct. *Simalia* Gray (1849), *Aspidopython* A. B. Meyer (1874), and *Hypaspistes* D. Ogilby (1891) — all of which have *Boa amethistina* Schneider (1801), or synonyms of it, as type — are synonyms of *Liasis* Gray (1842), to which *amethistina* was transferred by Stull (1935).

1803. *Python* Daudin (part), Mag. Encycl. (March, An. 8), p. 434 and Hist. Nat. Rept., **5**, p. 226. Type by subsequent designation: *Coluber molurus* Linnaeus.

1830. *Constrictor* Wagler (not Laurenti:1768), Syst. Nat. Amphib., p. 168. Type by subsequent designation: *Boa reticulata* Schneider.

1842. *Heleionomus* Gray, Zool. Misc., p. 42. Type by monotypy: *H. variegatus* Gray = *Coluber sebae* Gmelin.

1842. *Hortulia* Gray, Zool. Misc., p. 43. Type by monotypy: *Python natalensis* A. Smith = *Coluber sebae* Gmelin.

1843. *Asterophis* Fitzinger, Syst. Rept., p. 24. Type by original designation: *Python tigris* Daudin = *Coluber molurus* Linnaeus.

1884. *Aspidoboa* Sauvage, Bull. Soc. Philom. Paris, (7) **8**, p. 143. Type by monotypy: *Python curtus* Schlegel.

Python sebae (Gmelin) Common African Python

1789. *Coluber Sebae* Gmelin, Syst. Nat., ed. 13, **1**, Part 3, p. 1118: (based on Seba, Thesaurus, **2**, pl. cxcix, fig. 2) "America" (error).

1789. *Coluber Speciosus* Bonnaterre, Encyl. Méthod. Règnes Nat., Ophiol., p. 17: "Brazil" (error).

1801. *Boa Hieroglyphica* Schneider, Hist. Amphib., **2**, p. 266: Cairo, Egypt (by inference as taken from Seba).

1803. *Python Houttuyni* Daudin, Hist. Nat. Rept., **5**, p. 254: No locality.

1833. *Python natalensis* A. Smith, S. African Quart. Journ., **2**, p. 64: Natal, South Africa.

1842. *Heleionomus variegatus* Gray, Zool. Misc., p. 43: No locality.

1845. *Python Liberiensis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 249: Liberia.

1936. *Python jubalis* Pitman, Uganda Journ., **3**, p. 211: Somalia ("material in the museum at Mogadiscio, though I am unaware of any published description." *nomen nudum*).

Range. Africa south of Senegal, the Sudan and Eritrea; including Uganda; Kenya Colony and Tanganyika Territory.

Subfamily BOINAE

Genus **ERYX** Daudin

1803. *Eryx* Daudin (part), Mag. Encycl. (March, An. 8), p. 437, and Hist. Nat. Rept., **7**, p. 251. Type by subsequent designation: *Boa turcica* Olivier.

1803. *Clothonia* Daudin, Hist. Nat. Rept., **7**, p. 283. Type by monotypy: *Boa anguiniformis* Schneider = *Boa johnii* Russell.

1830. *Gongylophis* Wagler, Nat. Syst. Amphib., p. 192. Type by monotypy: *Boa conica* Schneider.

1849. *Cusoria* Gray, Cat. Snakes Brit. Mus., p. 107. Type by monotypy: *C. elegans* Gray.

1864. *Cursoria* Günther, Rept. British India, p. 333. Emendation for *Cusoria* Gray.

Eryx colubrinus loveridgei Stull Kenya Sand-Boa

1932. *Eryx thebaicus loveridgei* Stull, Occ. Papers Boston Soc. Nat. Hist., **8**, p. 29, pl. ii, fig. B: "Mbunyi" i.e. Mbuyuni, Kenya Colony.

Range. Arid areas of Kenya Colony and northern Tanganyika Territory (at Kahe).[106]

Family COLUBRIDAE

Subfamily COLUBRINAE

Genus **BOTHROPHTHALMUS** Peters

1863. *Bothrophthalmus* Peters, Monatsb. Akad. Wiss. Berlin, p. 287. Type by monotypy: *Elaphis* (*Bothrophthalmus*) *lineatus* Peters.

Bothrophthalmus lineatus lineatus (Peters)
Red-and-Black Striped Snake

1863. *Elaphis* (*Bothrophthalmus*) *lineatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 287: Guinea.

1863. *Bothrophthalmus melanozostus* Jan, Elenco Sist. Degli Ofidi, p. 62: Gold Coast.

Range. Uganda, southwest through Belgian Congo to Angola, northwest (but with local races in the Cameroons) to French Guinea.

Genus **LYCODONOMORPHUS** Fitzinger

1843. *Lycodonomorphus* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Coronella rufula* Schlegel = *Coluber rufulus* Lichtenstein.

1848. *Lycodontomorphus* Agassiz, Nomen. Zool., Index Universalis, p. 628. Emend. for *Lycodonomorphus* Fitzinger.

1863. *Neusterophis* Günther, Proc. Zool. Soc. London, p. 16, footnote. Type by monotypy: *Natrix laevissima* Günther.

1893. *Ablabophis* Boulenger, Cat. Snakes Brit. Mus., **1**, p. 318. Type by

[106] While the "Uganda" specimen in the Museum of Comparative Zoology possibly came from that country, as it was bought from a dealer in the days of the "Uganda Railway," it may have come from Voi where the species is relatively common in the vicinity of the railway station.

monotypy: *Coluber rufulus* Lichtenstein.

1893. *Glypholycus* Günther, Proc. Zool. Soc. London, p. 629. Type by monotypy: *G. bicolor* Günther.

1924. *Nerophidion* Werner, Sitzb. Akad. Wiss. Wien, **133**, Abt. 1, p. 53.. Type by monotypy: *N. hypsirhinoides* Werner = *Glypholycus bicolor* Günther.

Lycodonomorphus bicolor (Günther)

Tanganyika White-bellied Water-Snake

1893. *Glypholycus bicolor* Günther, Proc. Zool. Soc. London, p. 629, fig. —: Lake Tanganyika.

1924. *Nerophidion hypsirhinoides* Werner, Sitzb. Akad. Wiss. Wien, **133**, Abt. 1, p. 53: No locality.

Range. Lake Tanganyika, Tanganyika Territory; also in lake off Northern Rhodesia; Belgian Congo and Ruanda-Urundi.

Lycodonomorphus rufulus whytii (Boulenger)

Whyte's Water-Snake

1897. *Glypholycus whytii* Boulenger, Proc. Zool. Soc., London, pp. 800, 802, pl. xlvi, fig. 2: Fort Hill, Nyasaland.

Range. Southern Tanganyika Territory and northern Nyasaland, south (? down eastern side of Lake Nyasa) to the Zambezi, Mozambique.

Genus **BOAEDON** Duméril & Bibron

1854.[107] *Boaedon* Duméril & Bibron, Erpét. Gén., **7**, p. 357. Type by present designation: *B. lineatum* Duméril & Bibron.

1854. *Eugnathus* Duméril & Bibron, Erpét. Gén., **7**, p. 406. Type by monotypy: *Lycodon geometricus* Schlegel.

1854. *Alopecion* Duméril & Bibron, Erpét. Gén., **7**, p. 416. Type by monotypy: *A. annulifer* Duméril & Bibron = *Lycodon guttatus* A. Smith.

1856. *Holuropholis* A. Duméril, Revue Mag. Zool. (2), **8**, p. 465. Type by monotypy: *H. olivaceus* A. Duméril.

1885. *Catapherodon* Rochebrune, Faune Senegambie, Rept., p. 186. Type by present designation: *Boaedon unicolor* Duméril & Bibron = *Lycodon fuliginosus* Boie.

1893. *Theleus* Cope, American Nat., **27**, p. 482. Type by monotypy: *Coelopeltis virgata* Hallowell.

[107] Boulenger (1893, Cat. Snakes Brit. Mus., **1**, p. 327) gives 1853 when the Mem. Acad. Sci. Paris, **23**, pp. 399-536 (reprint pp. 1-140), pls. i-ii, publlshed M. Duméril's "Prodome de la Classification des Reptiles Ophidiens." But A. M. C. Duméril there (p. 460) used only Boédon, the French form of the word, as was also the case with Eugnathes (p. 461) and Alopécion (p. 462).

Boaedon fuliginosus fuliginosus (Boie)[108]
Common House-Snake

1827. *Lycodon fuliginosus* Boie, Isis von Oken, **20**, col. 551: "Java" (error).

1837. *Lycodon unicolor* Schlegel (not Boie), Essai Phys. Serpents, **1**, p. 142; **2**, p. 112: Guinea Coast.

1854. *Boaedon Lineatum* Duméril & Bibron, Erpét. Gén., **7**, p. 363: Gold Coast.

1857. *Boaedon quadrivittatum* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 54: Isles de Los, off French Guinea.

1859. *Boaedon quadrilineatum* A. Duméril, Arch. Mus. Hist. Nat. (Paris), **10**, p. 193, fig. 4: Bissau, Portuguese Guinea.

1867. *Alopecion variegatum* Bocage, Jorn. Sci. Lisboa, **1**, p. 230: Benguela and Novo Redondo, Angola.

1888. *Boodon bipraeocularis* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 330, pl. xviii, fig. B: Lake Tanganyika; and Rabai Hills, Kenya Colony.

1902. *Boodon lineatus* var. *plutonis* Werner, Verh. Zool. Bot. Ges. Wien, **52**, p. 334: Boké, Rio Nunez, French Guinea.

1932. *Boaedon maculatus* Parker, Proc. Zool. Soc. London, p. 363: Bihen, 1500 feet, 8° 25′ N., 48° 25′ E., British Somaliland.

Range. Eritrea, south through Uganda; Kenya Colony; Tanganyika Territory; Pemba; Zanzibar and Mafia Islands to Natal, west to the Cape, north (except for Southwest Africa where *B. f. mentalis* Günther occurs) and west to Senegal east to Eritrea.

Boaedon olivaceus (Duméril) Gaboon Water-Snake

1856. *Holuropholis olivaceus* A. Duméril, Revue Mag. Zool. (2), **8**, p. 466: Gabon, French Congo.

Range. Uganda, southwest through the Belgian Congo to Angola, north and west to French Guinea.

Genus **LYCOPHIDION** Fitzinger

1843. *Lycophidion* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Lycodon horstokii* Schlegel = *L. capensis* A. Smith.

1844. *Lycophydion* Agassiz, Nomen. Zool., Rept., p. 27. Emendation for

[108] Unfortunately there seems to be no way of avoiding the unwelcome fact that this name should be used for what is probably the commonest of African snakes. In part the species owes its lengthy synonymy to the variability of its coloration, the young usually differing from the adults: though at times the adults may retain the juvenile coloring, they are generally bright brown, dark brown or black. So far I have failed to separate an East African race, but trinomials are necessary as races occur in the rain-forests of West Africa (*B. f. virgatus* (Hallowell) Cameroons to Liberia), arid areas of Southwest Africa (*B. f. mentalis* Günther), and also of Arabia (*B. f. arabicus* Scortecci: if distinct).

Lycophidion Fitzinger:1843.

1857. *Lycophidium* Agassiz, Nomen. Zool., Index Univers., p. 218. Emendation for *Lycophydion* Agassiz:1844.

1857. *Lissophis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 59. Type by original designation: *L. laterale* Hallowell.

1858. *Metoporhina* Günther, Cat. Snakes Brit. Mus., p. 197. Type by monotypy: *Coluber irroratus* Leach.

Lycophidion meleagris Boulenger Speckled Wolf-Snake

1893. *Lycophidium meleagris* Boulenger, Cat. Snakes Brit. Mus., **1**, p. 337, pl. xxi, fig. 2: Ambriz and Ambrizette, Angola.

Range. Usambara; Magrotto and Uluguru Mountains, Tanganyika Territory, west through the Belgian Congo to Angola.

Lycophidion capense ornatum Parker Ornate Wolf-Snake

1936. *Lycophidion ornatum* Parker, Novit. Zool. (Tring), **40**, p. 122: Congulu, Angola.

Range. Virgin forests of Uganda; western Kenya Colony and western Tanganyika Territory, west through Belgian Ruanda-Urundi and the Belgian Congo to Angola. Also Gold Coast (M.C.Z. 49606, etc.).

Lycophidion capense uzungwense Loveridge
Red-snouted Wolf-Snake

1932. *Lycophidion capense uzungwensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 375: Dabaga, Uzungwe Mountains, Tanganyika Territory.

Range. Uplands of northwestern (at Kibondo) and southern Tanganyika Territory.

Lycophidion capense capense (Smith)[109]
Common Wolf-Snake

1831. *Lycodon capensis* A. Smith, S. African Quart. Journ., **1**, p. 18: "Kurrichane," i.e. Rustenberg district, Transvaal.

1837. *Lycodon horstokii* Schlegel, Essai Phys. Serp., **2**, p. 111, pl. iv, figs. 10-11: Cape of Good Hope in the uncultivated parts near the frontiers of Kaffraria (restricted).

1888. *Lycophidium Capense* mut. *multimaculata* Boettger, Ber. Senekenberg, Naturf. Ges., p. 67: Povo Nemlao and Povo Netonna, near Banana, Belgian Congo.

1893. *Lycophidium jacksoni* Boulenger, Cat. Snakes Brit. Mus., **1**, p. 340, pl. xxi, fig. 3: Mount Kilimanjaro, Tanganyika Territory; Lamu, Kenya Colony.

1893. *Lycophidium abyssinicum* Boulenger, Cat. Snakes Brit. Mus., **1**, p. 342, pl. xxii, fig. 1: Southern Abyssinia.

Range. Egypt (Fayum only), east to Arabia, south through Uganda; Kenya Colony; Tanganyika Territory; Pemba and Zanzibar Islands;[109] to Natal, west to the Cape, northwest to French Guinea (possibly Portuguese Guinea and Senegal if *L. c. gambiense* Rochebrune is included).

Genus **HORMONOTUS** Hallowell

1857. *Hormonotus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 56. Type by monotypy: *H. audax* Hallowell = *Lamprophis modestus* Duméril & Bibron.

Hormonotus modestus (Duméril & Bibron)

1854. *Lamprophis modestus* Duméril & Bibron, Erpét. Gén., **7**, p. 429: Guinea.

1857. *Hormonotus audax* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 56: Gabon, French Congo.

1863. *Heterolepis glaber* Jan, Elenco Sist. Degli Ofidi, p. 98: Boutry, Ashanti, Gold Coast.

1888. *Boodon* (*Alopecion*) *Vossii* Fischer, Jahrb. Hamburg. Wiss. Anst., **5**, p. 3, pl. i, fig. 1: Cameroon.

Range. Uganda, southwest through Belgian Congo to Angola, northwest to French Guinea.

[109] Parker (1949, Zool. Verh. Rijksmus. Nat. Hist. Leiden, No. 6, pp. 54-56) points out that it is doubtful whether the types of *acutirostre* Günther (1868, Ann. Mag. Nat. Hist., (4) 1, p. 427, pl. xix, fig. D), though sent by Sir John Kirk *from* Zanzibar, originated there, for in a letter from Sir John (1867, Proc. Zool. Soc. London, p. 952) he states he had a "valuable collection of snakes and insects *from Mozambique*" (italics H.W.P.). The collection was received at the British Museum in 1868. Parker adds that since 1867 no wolf-snakes with such low scale-counts as the cotypes of *acutirostre* have been taken on Zanzibar Island. To which I might add that the sexing of some as given in the catalogue (1893, p. 338) is in error. In removing *L. c. acutirostre* from this check list it is as well to draw attention to the fact that in the non-montane coastal belt of East Africa there is a population of *capense* which can be separated from the more or less white-throated *c. capense* of the interior by their uniformly blackish-brown throat and undersurfaces. The Museum of Comparative Zoology has such specimens from Kibwezi; foot of Mbololo; Malindi; Changamwe near Mombasa (seen); Kilosa; Morogoro; Bagamoyo; Zanzibar; Dar es Salaam; Mbanja near Lindi; Liwale; Tunduru and Ugano.

Parker mentions that the British Museum specimen with the lowest counts (♀ :V.156 :C.20) is from Kosi Bay, Zululand. Presumably the same snake that in 1908 Boulenger referred to *semiannulis* Peters, with the qualification that it lacked the dark crossbars of the type from Tete, Mozambique. This was precisely the case with the eight snakes (3 ♂♂, 5 ♀♀ :V.130-144 ;C.24-31) that I personally captured at Lumbo, Mozambique and referred to *semiannulis* in 1923. If *acutirostre* came from *Mozambique* it is highly probable that the Lumbo snakes represent the same thing. This suggests that *acutirostre* may be a synonym of *semiannulis* which — except for a very questionable Angola record of 1898 — has not been taken since Peters described it over a hundred years ago. I failed to find any *Lycophidion* during the month that I spent at Tete in 1949.

Genus **MEHELYA** Csiki

1847. *Heterolepis* A. Smith (not Nees:1834), Illus. Zool. S. Africa, Rept., footnote to pl. lv. Type by original designation: *H. capensis* A. Smith.

1858. *Simocephalus* Günther (not Schodler:ix.1858), 9.x.1858, Cat. Snakes Brit. Mus., p. 194. New name for *Heterolepis* Smith (preoccupied).

1903. *Grobbenia* Poche (not Holdhaus:28.vii.1903), 21.ix.1903, Zool. Anz., **26**, p. 699. Type by original designation: *Heterolepis poensis* A. Smith.

1903. *Méhelya* Csiki, 15.xi.1903, Rovartani Lapok, p. 198, footnote. New name for *Grobbenia* Poche (preoccupied).

1904. *Siebenrockia* Poche, 13.ix.1904, Zool. Anz., **28**, p. 38. New name for *Grobbenia* Poche (preoccupied).

Mehelya capensis savorgnani (Mocquard)

Northwestern Cape File-Snake

1887. *Heterolepis Savorgnani* Mocquard, Bull. Soc. Philom. Paris, (7) **11**, p. 27, pl. ii, figs. 4-4b: Ogooué River, French Congo.

1893. *Simocephalus chanleri* Stejneger, Proc. U. S. Nat. Mus., **16**, p. 726: Wange, *opposite* Manda Island, Kenya Colony.

1901. *Simocephalus phyllophis* Werner, Zool. Anz., **24**, p. 301, figs. 3-4: Cameroon.

1907. *Simocephalus Butleri* Boulenger, Ann. Mag. Nat. Hist., (7) **20**, p. 489: Between Wau and Chakchak, Bahr el Ghazal Province, Sudan.

1910. *Simocephalus unicolor* Boulenger, Ann. Mag. Nat. Hist., (8) **5**, p. 512: Fort Hall, Kenya Colony.

1910. *Mehelya* (or *Simocephalus*) *lamani* Lönnberg, Arkiv. Zool., **7**, No. 8, p. 1: Mukimbungu, lower Congo River, Belgian Congo.

1913. *Mehelya* (*Simocephalus*) *somaliensis* Lönnberg & Andersson, Arkiv. Zool., **8**, No. 20, p. 2: "Kismayu," i.e. Chisimaio, Somalia.

Range. Southern Sudan and southern Somalia, west through Kenya Colony; Uganda; Belgian and French Congo to French Cameroon.

Mehelya capensis capensis (Smith)

Southeastern Cape File-Snake

1847. *Heterolepis capensis* A. Smith, Illus. Zool. S. Africa, Rept., pl. lv: Eastern districts of Cape Province, South Africa.

1874. *Heterolepis Gueinzii* Peters, Monatsb. Akad. Wiss. Berlin, p. 164, pl. —, fig. 2: Port Natal, *i.e.* Durban, Natal.

Range. Tanganyika Territory,[110] south through Nyasaland to Natal, west through Bechuanaland to Angola.

Mehelya poensis (Smith) Western-Forest File-Snake

1847. *Heterolepis poensis* A. Smith, Illus. Zool. S. Africa, Rept., footnote to pl. lv: Fernando Po.

1854. *Heterolepis bicarinatus* Duméril & Bibron, Erpét. Gén., **7**, p. 422: Fernando Po.

Range. Uganda southwest through Belgian Congo to Angola, northwest to French Guinea.[110]

Mehelya stenophthalmus (Mocquard) Small-eyed File-Snake

1887. *Heterolepis stenophthalmus* Mocquard, Bull. Soc. Philom. Paris, (7) **11**, p. 16, pl. i, figs. 1-1b: Assini, Gold Coast and Cape Lopez, French Congo.

1911. *Gonionotophis microps* Boulenger, Ann. Mag. Nat. Hist., (8) **8**, p. 370: Bitye, French Cameroon.

Range. Uganda, west through Belgian Congo to Gold Coast: Portuguese Guinea.

Mehelya nyassae (Günther) Nyasaland File-Snake

1888. *Simocephalus nyassae* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 328: Lake Nyasa, Nyasaland.

1906. *Gonionotophis degrijisi* Werner, Zool. Anz., **30**, p. 53: Usambara Mountains, Tanganyika Territory.

Range. Kenya Colony (Tana River:A.L.); Tanganyika Territory and Zanzibar Island, south through Mozambique, Nyasaland and Southern Rhodesia to the Transvaal and Natal. Also Belgian Ruanda-Urundi.

Genus **GEODIPSAS** Boulenger[111]

1896. *Geodipsas* Boulenger, Cat. Snakes Brit. Mus., **3**, p. 32. Type by present designation: *Tachymenis infralineatus* Günther.

Geodipsas vauerocegae Tornier Usambara Forest-Snake

1902. *Geodipsas vauerocegae* Tornier, Zool. Anz., **25**, p. 703: Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of the Usambara; Magrotto and Uluguru Mountains, Tanganyika Territory.

Geodipsas procterae Loveridge Uluguru Forest-Snake

[110] Voeltzkow's listing of *"poensis"* from Zanzibar is assumed to have been based on misidentified *c. capensis* from coastal Tanganyika (= Zanzibar auct.).

[111] Snakes of this genus possess (1) hypapophyses on the posterior vertebrae; (2) grooved maxillary teeth; (3) a forked sulcus spermaticus. In the last two characters they differ from *Natriciteres* to which they bear at least a superficial resemblance. Other species occur in the Cameroons and in Madagascar.

1922. *Geodipsas procterae* Loveridge, Proc. Zool. Soc. London, p. 313: Uluguru Mountains, Tanganyika Territory.

Range. Virgin forests of the Uluguru Mountains, Tanganyika Territory.

Genus **NATRICITERES** Loveridge[112]

1953. *Natriciteres* Loveridge, Bull. Mus. Comp. Zool., **110**, p. 248. Type by original designation: *Coronella olivacea* Peters.

Natriciteres olivacea olivacea (Peters) Olive Marsh-Snake

1854. *Coronella olivacea* Peters, Monatsb. Akad. Wiss. Berlin, p. 622: Tete, Mozambique.

1860. *Coronella* (*Meizodon*) *dumerilii* Günther, Proc. Zool. Soc. London, p. 429, fig. —: "Sierra Leone" (error, *fide* Boulenger, for Gold Coast).

1863. *Enicognathus punctatostriatus* Jan, Arch. Zool. Anat. Fisiol., **2**, p. 278: Type in Hamburg Museum, but no locality.

1877. *Neusterophis atratus* Peters, Monatsb. Akad. Wiss. Berlin, p. 614, pl. —, fig. 1: Chinchoxo, Cabinda.

1886. *Grayia Giardi* Dollo, Bull. Mus. Roy. Hist. Nat. Belgique, **4**, p. 158, figs. 1-2: Lake Tanganyika region, Belgian Congo.

Range. Sudan east to Somalia, south through Uganda; Kenya Colony; Tanganyika Territory; Zanzibar and Mafia Islands to southern Rhodesia, northwest through Belgian Congo to the Gold Coast.

Natriciteres olivacea uluguruensis (Loveridge) Montane Marsh-Snake

1935. *Natrix olivacea uluguruensis* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 7: Nyange, Uluguru Mountains, Tanganyika Territory.

Range. Montane forests and marshes of Tanganyika Territory, south to southern Rhodesia, west to Angola.

Natriciteres olivacea pembana (Loveridge)[113] Pemba Island Marsh-Snake

1935. *Natrix olivacea pembana* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 8: Chakechake, Pemba Island.

Range. Pemba Island.

[112] The eight generic names that have been misapplied to snakes of this genus, are listed under the original (1953) citation of *Natriciteres*.

[113] A possibly untenable race depending on whether a majority of Pemba snakes have 15 midbody scale-rows: occasional individuals of the mainland *montane* form have 15.

Genus **COLUBER** Linnaeus[114]

1758. *Coluber* Linnaeus, Syst. Nat. ed. 10, **1**, p. 216: Type by designation of Fitzinger:1843: *C. constrictor* Linnaeus.

1818. *Scoliophis* Lesueur, Journ. Phys. Chim. Hist. Nat., **86**, p. 297, Type by monotypy: *S. atlanticus* Lesueur = *Coluber constrictor* Linnaeus.

1826. *Hemorrhois* Boie, Isis von Oken, **19**, col. 982. Type by original designation: *Coluber hippocrepis* Linnaeus.

1830. *Periops* Wagler, Nat. Syst. Amphib., p. 189. Type by monotypy: *Coluber hippocrepis* Linnaeus (inc. *Natrix bahiensis* Wagler).

1843. *Hierophis* Fitzinger, Syst. Rept., p. 26. Type by original designation: *Coluber viridiflavus* Lacépède.

1844. *Haemorrhois* Agassiz, Nomen. Zool., Rept., p. 20. Emendation for *Hemorrhois* Boie.

1853. *Bascanion* Baird & Girard, Cat. N. American Rept., p. 93. Type by subsequent designation: *Coluber constrictor* Linnaeus.

1854. *Coryphodon* Duméril & Bibron (part; not Owen:1845), Erpét. Gén., **7**, p. 180. Type by subsequent designation: *Coluber capistratus* Lichtenstein.

1860. *Platyceps* Blyth, Journ. Asiatic Soc. Bengal, **29**, p. 114. Type by monotypy: *P. subfasciatus* Blyth = *Coluber ventromaculatus* Gray.

1862. *Bascanium* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 338. Emendation for *Bascanion* Baird & Girard.

1865. *Megablabes* Günther, Ann. Mag. Nat. Hist., (3) **15**, p. 92. Type by monotypy: *M. olivaceus* Günther = *Herpetodryas dipsas* Schlegel.

1868. *Dolichophis* Gistel, in Blicke, Leben Natur Menschen (Leipzig), p. 155. Type (*fide* Mertens:1936): *Coluber caspius* Gmelin.

[114] *Coluber*, as employed here, is substantially the equivalent of "*Zamenis* Wagler" as used by Boulenger (1893, Cat. Snakes Brit. Mus., 1, p. 379). Unfortunately the type of *Zamenis* Wagler was designated by Fitzinger (1843, Syst. Nat., p. 26) as *Z. aesculapii* Wagler, a species that author specifically stated is the *Coluber aesculapii* of Lacépède, *not* of Linnaeus. This *C. aesculapii* Lacépède is commonly regarded as a synonym of what is now known as *Elaphe longissimus* Laurenti, so that *Zamenis* Wagler is primarily a synonym of *Elaphe* Fitzinger (1833, in Wagler, Descr. Icon. Amphib., text to pl. xxvii), whose type is *parreysii* Fitzinger = *Coluber quatuorlineatus* Lacépède.

Subsequent designation of *Natrix gemonensis* Laurenti as a type for *Zamenis* Wagler, by Ortenburger (1928), Malcolm Smith (1943), also Inger and Clark (1943, Copeia, p. 143) is therefore untenable, and *Zamenis* Wagler is a synonym of *Coluber* only "in part."

Probably other names should be added to those listed here in the synonymy of *Coluber*. Four of them (together with "*Zamenis*") are regarded as subgenera by Inger and Clark (*loc. cit.*). On the other hand, *Chilolepis* Fitzinger, 1843, Syst. Rept., p. 26 (of which *Coluber cliffordi* Schlegel is the type by original designation) together with its synonyms *Spalerosophis* Jan, 1865, in De Fillipi, Viagg. Persia, p. 356 (whose type was designated as *S. microlepis* Jan in 1930 by K. P. Schmidt when reviving *Spalerosophis*) and *Loxodon* (also *Toxodon*) Jan, 1867, are removed from the synonymy as the *Chilolepis* group appears to warrant generic status.

1895. *Acanthocalyx* Cope, Trans. Amer. Philos. Soc., **18**, p. 204. Type by original designation: *Coluber ventromaculatus* Gray.

1895. *Tylanthera* Cope, Trans. Amer. Philos. Soc., **18**, p. 205. Type by monotypy: *Coluber florulentus* Geoffroy.

1924. *Argyrogena* Werner, Sitzb. Akad. Wiss. Wien, **133**, Abt. 1, p. 51. Type by monotypy: *A. rostrata* Werner = *Coluber fasciolatus* Shaw.

Coluber keniensis Parker Lake Baringo Snake

1932. *Coluber keniensis* Parker, Journ. Linn. Soc. London, Zool., **38**, p. 220: Lake Baringo, Kenya Colony.

Range. Kenya Colony (known only from the holotype).

Coluber citernii (Boulenger) Somalia Snake

1912. *Zamenis citernii* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova (3), **5**, p. 331: Dolo, Somalia.

Range. Southern Somalia and northern Kenya Colony.[115]

Coluber florulentus smithi (Boulenger)[116]
Southern Flowered-Snake

1895. *Zamenis smithi* Boulenger, Proc. Zool. Soc. London, p. 536, pl. xxx, fig. 2: Shebeli River, Somalia.

1935. *Coronella semiornata fuscorosea* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 8: Mount Mbololo, Teita, Kenya Colony.

Range. Ethiopia and Somalia, south to Kenya Colony.

Genus **MEIZODON** Fischer

1856. *Meizodon* Fischer, Abhand. Naturw. Ver. Hamburg, **3**, p. 112. Type by monotypy: *M. regularis* Fischer = *Calamaria coronata* Schlegel.

Meizodon semiornatus semiornatus (Peters)[117]
Southern Semiornate-Snake

[115] Here reported from Kenya for the first time on the basis of a ♀ (M.C.Z. 51691) from Malca Murri with 21 midbody scale-rows; 219 ventrals; a divided anal; 87 subcaudals; 8 labials, the 4th and 5th enterlng the orbit. Total length 570 (432 + 138) mm. This snake unquestionably represents *citernii*, previously known only from the holotype.

[116] The 1896 record of *"smithii"* from Assab, Eritrea, is assumed to be based on a *C. f. florulentus* Geoffroy. Conversely, the *"florulentus"* recorded by Lönnberg (1911) from just north of the Uaso Nyiro (as Guaso Nyiri), and also a Lake Rudolf snake in the Nairobi Museum are almost certainly *C. f. smithi*, which I still think is only a race.

[117] Trinomials are employed on account of a northern race — *M. s. plumbeiceps* (Boettger:1893) with *somalica* (Scortecci:1932) and *loveridgei* Bogert:1940 as synonyms — ranging from Sudan, Ethiopia and British Somaliland south through Somalia. Where the races actually meet remains to be defined, probably arbitrarily, as the sole character separating them appears to be the predominance of 1 + 2 temporals in the northern race, 2 + 2 in the southern. The Uganda record of Boulenger (1902) is extremely questionable as no specimen is known.

1854. *Coronella semiornata* Peters, Monatsb. Akad. Wiss. Berlin, p. 622: Tete, Mozambique.

1879. *Zamenis fischeri* Peters, Monatsb. Akad. Wiss. Berlin, p. 777: Malindi, Kenya Colony.

1884. *Coronella inornata* Fischer, Jahrb. Hamburg. Wiss. Anst., **1**, p. 6, pl. i, fig. 2: Masailand, Kenya Colony.

1908. *Coronella scheffleri* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 93: Kibwezi, Kenya Colony.

1935. *Coronella semiornata* var. *mossambica* Cott, Proc. Zool. Soc. London, 1934, p. 967: Charre and Fambani, Mozambique.

Range. Uganda; Kenya Colony and Tanganyika Territory, south through Mozambique to Nyasaland and the Rhodesias.

Meizodon coronatus (Schlegel) Western Crowned-Snake

1837. *Calamaria coronata* Schlegel, Essai Phys. Serp., **2**, p. 46: Gold Coast.

1856. *Meizodon regularis* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 112, pl. iii, fig. 3: Peki, Gold Coast.

1858. *Coryphodon margaritiferus* Günther, Cat. Snakes Brit. Mus., p. 109: West Africa.

1860. *Coronella* (*Meizodon*) *bitorquata* Günther, Proc. Zool. Soc. London, p. 428, fig. —: Senegal.

1863. *Coronella elegans* Jan, Arch. Zool. Anat. Fisiol., **2**, p. 255: No locality.

1917. *Zamenis tchadensis* Chabanaud, Bull. Mus. Hist. Nat. (Paris), **22**, p. 451, figs. 3-5: Koalem, French West Africa.

1933. *Coronella regularis praeornata* Angel, Serpentes Afrique Occ. Française, p. 123, figs. 45a-b: French Sudan and Uganda.

1951. *Meizodon coronata camerunensis* Monard, Mem. Inst. Franc. Afrique Noire (Sci. Nat.), No. 1, pp. 151, 161: Konn, French Cameroon.

Range. Kenya Colony and Uganda, west in equatorial belt (5° S. to 15° N.) to Senegal.

Genus **PHILOTHAMNUS** Smith[118]

1847. *Philothamnus* A. Smith, Illus. Zool. S. Africa, footnote to text for pl. lix. Type by monotypy: *Dendrophis* (*Philothamnus*) *semivariegata* A. Smith.

1857. *Chlorophis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 53. Type by monotypy: *C. heterodermus* Hallowell.

1866. *Herpetaethiops* Günther, Ann. Mag. Nat. Hist., (3) **18**, p. 27. Type

[118] *Chlorophis* Hallowell is regarded as a subgenus, usually recognizable by the absence of a sharply angular subcaudal keel along either side of the tail.

by monotypy: *H. bellii* Günther = *Chlorophis heterodermus* Hallowell.

1868. *Chlorophis* Theobald (not Hallowell), Cat. Rept. Asiatic Soc. Mus., p. 49. Type by monotypy: *C. oldhami* Theobald = *Ahaetulla hoplogaster* Günther.

1895. *Oligolepis* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 171. Type by monotypy: *O. macrops* Boulenger.

Philothamnus macrops (Boulenger) Usambara Green-Snake

1895. *Oligolepis macrops* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 171: Usambara Mountains, Tanganyika Territory.

Range. Coastal Tanganyika Territory and Zanzibar Island.

Philothamnus heterodermus carinatus (Andersson) Thirteen-scaled Green-Snake

1901. *Chlorophis carinatus* Andersson, Svenska Vetensk.-Akad. Hand., **27**, No. 5, p. 9: Mapanja, British Cameroon.

Range. Western Kenya Colony and Uganda, west through Belgian Congo to Fernando Po.

Philothamnus hoplogaster (Günther) Southeastern Green-Snake

1863. *Ahaetulla hoplogaster* Günther, Ann. Mag. Nat. Hist., (3) **11**, pp. 284, 286: "Port Natal," *i.e.* Durban, Natal.

1866. *Philothamnus neglectus* Peters, Monatsb. Akad. Wiss. Berlin, p. 890, footnote: "Prazo Boror," *i.e.* Boror, Mozambique.

1868. *Chlorophis Oldhami* Theobald, Cat. Rept. Asiatic Soc. Mus., p. 49: "Simla, India" (error).

Range. Tanganyika Territory (south of the Usambara Mountains), south through Mozambique and the Rhodesias to Port Elizabeth, Cape Province, South Africa.

Philothamnus irregularis battersbyi Loveridge[119] Northeastern Green-Snake

1951. *Philothamnus irregularis battersbyi* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 51: Sipi Forest at 6000 feet on Elgon Mountain, eastern Uganda.

Range. Sudan (east of the Nile), east through Ethiopia to Somalia, south through Uganda and Kenya Colony to (and including) the Usambara Mountains, Tanganyika Territory, west to Lake Victoria.

[119] This is the common green-snake of the northeastern savannas which, with the preceding has been so long erroneously known as *Chlorophis neglectus* (Peters).

Philothamnus irregularis irregularis (Leach)
Western Green-Snake

1789. *Coluber Caeruleus* Lacépède (not Linnaeus), Hist. Nat. Serpens, **2**, Table Methodique, p. 100, text p. 276: Cap Vert, Senegal.
1802. *Coluber caerulescens* Daudin (not Linnaeus: new name for *caeruleus* Lacépède), Hist. Nat. Rept., **7**, p. 54.
1818. *Coluber caesius* Cloquet[120] (new name for *caeruleus* Lacépède), Dict. Sci. Nat. (Paris) **11**, p. 201.
1819. *Coluber irregularis* Leach, in Bowdich, Miss. Ashantee, App. p. 494: "Fantee," i.e. Fanti, Ashanti, Gold Coast.
1843. *Dendrophis Chenonii* Reinhardt, Dansk. Vidensk. Selsk. Skrift., **10**, p. 246, pl. i, figs. 13-14: Guinea.
1848. *Dendrophis* (*Philothamnus*) *albo-variata* A. Smith, Illus. Zool. S. Africa, Rept., pl. lxiv, figs. 3-3b; pl. lxv: South Africa towards Tropic of Capricorn (also Gold Coast; Sierra Leone; Gambia).
1875. *Philothamnus irregularis* var. *longifrenatus* Buchholz and Peters, Monatsb. Akad. Wiss. Berlin, p. 199: Cameroon.
1882. *Philothamnus angolensis* Bocage, Jorn. Sci. Lisboa, **9**, p. 7: Capangombe, Angola.
1888. *Ahaetulla emini* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 51: "Monbuttu," *i.e.* Mangbetu, Belgian Congo.
1888. *Ahaetulla shirana* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 326: Blantyre Mission, Shire River, Nyasaland.
1893. *Philothamnus Güntheri* Pfeffer, Jahrb. Hamburg. Wiss. Anst., **10**, p. 85, pl. i, figs. 3-5: Quilimane, Mozambique.
1932. *Chlorophis vernayi* FitzSimons, Ann. Transvaal Mus., **15**, p. 38: Maun, Thamalakane River, British Bechuanaland.

Range. In addition to western Uganda and western Tanganyika Territory: West and Central Africa south of 15° N. and north of 20° S. but following the Zambezi to the East Coast. More specifically: Senegal east to Metemma (introduced) on the White Nile south down the Rift Valley (Lakes Victoria, Tanganyika and both sides of Nyasa) into Southern Rhodesia, west to Damaraland, northwest to Senegal.

Philothamnus heterolepidotus (Günther) Slender Green-Snake

1863. *Ahaetulla heterolepidota* Günther, Ann. Mag. Nat. Hist., (3) **11**, p. 286: Africa.
1888. *Ahaetulla gracillima* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 326: Lower Congo River, Belgian Congo.

[120] Suppressed by the International Commission on Zoological Nomenclature in 1955. See Opinions and Declarations, **9**, pp. 299-308.

1910. *Chlorophis gracilis* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 64: Dodo, French Cameroon.

1912. *Chlorophis schubotzi* Sternfeld, Wiss. Ergebn. Deutsch. Zentral-Afrika-Exped. 1907-1908, **4**, p. 269, fig. 4: Bwanja, near Bukoba, Tanganyika Territory.

1923. *Chlorophis bequaerti* Schmidt (part), Bull American Mus. Nat. Hist., **49**, p. 75, fig. 3: Niangara, Belgian Congo (based on an aberrant *heterolepidotus* ♂ with entire anal = the holotype; omit paratype ♀, a similarly aberrant *irregularis*).

Range. Southern Sudan; Uganda and western Kenya Colony, southeast to mouth of the Rovuma River, Tanganyika Territory; (? Mozambique); west to Angola and northwest to Togo.

Philothamnus semivariegatus dorsalis (Bocage)[121]

Striped Wood-Snake

1866. *Leptophis dorsalis* Bocage, Jorn. Sci. Lisboa, **1**, pp. 48, 69: Molembo, Loanda Coast, Angola (restricted by Bocage:1882).

Range. Angola, north to the Belgian and French Congo.

Philothamnus semivariegatus semivariegatus (Smith)

Spotted Wood-Snake

1847. *Dendrophis* (*Philothamnus*) *semivariegata* A. Smith, Illus. Zool. S. Africa, pls. lix; lx; lxiv, figs. 1a-1b: Bushman Flat, Cape Province, South Africa (restricted by Bogert:1940).

1866. *Philothamnus punctatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 889: Zanzibar Coast, *i.e.* Tanganyika Territory.

1868. *Ahaetulla Kirkii* Günther, Ann. Mag. Nat. Hist., (4) **1**, p. 424: Zanzibar Island.

1869. *Dendrophis melanostigma* Jan, Icon. Gén. Ophid., livr. 32, pl. ii, fig. 3: Mozambique.

1882. *Philothamnus Smithii* Bocage, Jorn. Sci. Lisboa, **9**, p. 12, fig. 5: Bissau, Portuguese Guinea (hereby restricted A.L.).

1888. *Ahaetulla Bocagii* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 326: Angola.

1893. *Philothamnus punctatus* var. *sansibaricus* Pfeffer, Jahrb. Hamburg. Wiss. Anst., **10**, p. 83: Zanzibar Island.

Range. Includes Uganda; Kenya Colony; Tanganyika Territory; Pemba, Zanzibar and Mafia Islands. Africa south of 16° N. except forested areas bordering the Gulf of Guinea, certain

[121] It is very doubtful if this form should be admitted to the East African list. It is included here to invite attention to the population (of which I took 22 specimens) around Mwaya, Lake Nyasa, Tanganyika Territory. In this series the temporal arrangement was predominantly that of *dorsalis*, though in markings they resemble typical *semivariegatus* in lacking the vertebral stripe which is apparently not constant even among West African *dorsalis*.

islands therein and a vague coastal area from French Congo to Angola occupied by races, besides being absent from the Cape Peninsula region. More specifically Gambia east to Eritrea (though not recorded from Ethiopia), south to Natal and adjacent Cape Province, west and northwest (except for regions occupied by races) to Gambia.

Genus **HAPSIDOPHRYS** Fischer

1856. *Hapsidophrys* Fischer (part), Abhand. Nat. Ver. Hamburg, **3**, p. 110. Type by present designation: *H. lineatus* Fischer.

Hapsidophrys lineata Fischer Black-lined Green-Snake

1856. *Hapsidophrys lineatus* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 111, pl. ii, fig. 5: Elmina, Gold Coast.

1909. *Gastropyxis orientalis* Werner, Jahresb. Ver. Nat. Württemberg, (Stuttgart), **65**, p. 56: Tanganyika Territory.

Range. Western Kenya Colony and Tanganyika Territory, west through Uganda, southwest to Angola, north and west to French Guinea.

Genus **GASTROPYXIS** Cope

1861. *Gastropyxis* Cope, Proc. Acad. Nat. Sci. Philadelphia, 1860, pp. 556, 558. Type by monotypy: *Dendrophis smaragdina* Schlegel.

Gastropyxis smaragdina (Schlegel) Keel-scaled Green-Snake

1837. *Dendrophis smaragdina* Schlegel, Essai Phys. Serp., **2**, p. 237: Gold Coast.

1844. *Leptophis gracilis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 60: Liberia.

1856. *Hapsidophrys caerulens* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 111, pl. ii, fig. 6: Elmina, Gold Coast.

Range. Uganda, southwest through the Belgian Congo to Angola, north and west to Portuguese Guinea.

Genus **THRASOPS** Hallowell[122]

1857. *Thrasops* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 67. Type by monotypy: *Dendrophis flavigularis* Hallowell.

1862. *Rhamnophis* Günther, Ann. Mag. Nat. Hist., (3) **9**, p. 129. Type

[122] *Rhamnophis* is at best but a subgenus of *Thrasops*, the differences between the two being slight, as may be seen by comparing their respective characters given in my revision (1944, Bull. Mus. Comp. Zool., **95**, pp. 124-138).

by monotypy: *R. aethiopissa* Günther.

1864. *Crypsidomus* Günther, Proc. Zool. Soc. London, p. 309. Substitute name for *Rhamnophis* Günther.

Thrasops jacksonii jacksonii Günther

Western Black Tree-Snake

1895. *Thrasops Jacksonii* Günther, Ann. Mag. Nat. Hist., (6) **15**, p. 528: Kavirondo, Kenya Colony.

1905. *Thrasops Rothschildi* Mocquard, Bull. Mus. Hist. Nat. (Paris), **11**, p. 287: "Afrique orientale anglaise," i.e. Kenya Colony.

Range. Western Kenya Colony and Tanganyika Territory (west of Lake Victoria), west through Uganda to the Belgian Congo.

Thrasops jacksonii schmidti Loveridge

Eastern Black Tree-Snake

1936. *Thrasops jacksonii schmidti* Loveridge, Proc. Biol. Soc. Washington, **49**, p. 63: Meru Forest, Mount Kenya, Kenya Colony.

Range. Central Kenya Colony (virgin forests of Mount Kenya and Muthaiga near Nairobi).

Thrasops aethiopissa elgonensis (Loveridge)

1929. *Rhamnophis aethiopissa elgonensis* Loveridge, Bull. U. S. Nat. Mus., **151**, p. 24: Yala (= Lukosa) River, Kenya Colony.

Range. Western Kenya Colony to western Uganda.

Genus **SCAPHIOPHIS** Peters

1870. *Scaphiophis* Peters, Monatsb. Akad. Wiss. Berlin, p. 644. Type by monotypy: *S. albopunctatus* Peters.

Scaphiophis albopunctatus albopunctatus Peters

Gray Beaked-Snake

1870. *Scaphiophis albopunctatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 645, pl. i, fig. 4: Kita, French West Africa.

Range. Uganda; Kenya Colony and Tanganyika Territory, west through Belgian Congo to the French Soudan.

Genus **PROSYMNA** Gray

1849. *Prosymna* Gray, Cat. Snakes Brit. Mus., p. 80. Type by monotypy: *Calamaria melcagris* Reinhardt.

1849. *Temnorhynchus* A. Smith (not of Hope:1837), Illus. Zool. S.

Africa, Rept., App., p. 17. Type by monotypy: *T. sundewallii* (misprint for *sundevallii*) A. Smith.

1863. *Ligonirostra* Cope, Amer. Journ. Sci. Arts, (2) **35**, p. 457. New name for *Temnorhynchus* Smith (preoccupied in coleoptera).

1896. *Asthenophis* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2) **17**, p. 12. Type by monotypy: *A. ruspolii* Boulenger.

1902. *Pseudoprosymna* Lindholm, in Lampe, Jahrb. Nassau Ver. Naturk. (Wiesbaden), **55**, p. 57. Type by monotypy: *P. bergeri* Lindholm.

1909. *Stenorhabdium* Werner, Jahresb. Ver. Nat. Württemberg, **65**, p. 59. Type (believed lost) by monotypy: *S. temporale* Werner.

Prosymna pitmani Battersby Multi-scaled Shovel-snout

1951. *Prosymna pitmani* Battersby, Ann. Mag. Nat. Hist, (12) **4**, p. 828: Kilwa, Southern Province, Tanganyika Territory.

Range. Southeastern Tanganyika Territory.

Prosymna ambigua bocagii Boulenger
Central African Shovel-snout

1897. *Prosymna Bocagii* Boulenger, Ann. Mag. Nat. Hist., (6) **19**, p. 278, figs. —: Zongo, Ubangi Rapids, Belgian Congo.

Range. Southern Sudan and Uganda to northern and eastern Belgian Congo.

Prosymna ambigua stuhlmanni (Pfeffer)
East African Shovel-snout

1893. *Ligonirostra Stuhlmanni* Pfeffer, Jahrb. Hamburg. Wiss. Anst., **10**, p. 78, pl. i, figs. 8-10: Usambara, Tanganyika Territory.

1906. *Prosymna Vassei* Mocquard, Bull. Mus. Hist. Nat. (Paris), **12**, p. 250: Mozambique.

1909. *Prosymna variabilis* Werner, Jahresb. Ver. Nat. Württemberg, **65**, p. 57: Moshi, Tanganyika Territory.

1909. *Stenorhabdium temporale* Werner, Jahresb. Ver. Nat. Württemberg, **65**, p. 60: "East Africa."

Range. Coastal Kenya Colony; Tanganyika Territory and Zanzibar Island, south through Mozambique, Nyasaland and the Rhodesias to Zululand, Natal.

Prosymna ambigua ornatissima Barbour & Loveridge
Ornate Shovel-snout

1928. *Prosymna ornatissima* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 120, col. pl. ii, fig. 2: Nyange, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains Tanganyika Territory.

Genus **PSEUDASPIS** Fitzinger

1843. *Pseudaspis* Fitzinger, Syst. Rept., p. 25. Type by original designation: *Coluber canus* Linnaeus.

1868. *Cadmus* Theobald (not Bory:1824), Cat. Rept. Asiatic Soc. Mus., p. 58. Type by monotypy: *C. cuneiformis* Theobald = *Coluber canus* Linnaeus.

1882. *Ophirhina* Bocage, Jorn. Sci. Lisboa, **8**, p. 300. Type by monotypy: *O. anchietae* Bocage = *Coluber canus* Linnaeus.

Pseudaspis cana (Linnaeus) Mole Snake

1758. *Coluber canus* Linnaeus, Syst. Nat., ed. 10, **1**, p. 221: "in Indiis," i.e. Africa.

1768. *Coluber elegantissimus* Laurenti, Syn. Rept., p. 96: (based on Seba, Thesaurus, **1**, pl. lxxxi, fig. 9) No locality.

1789. *Coluber ocellatus* Gmelin, Syst. Nat., ed. 13, **1**, Part 3, p. 1113: (based on Seba, Thesaurus, **2**, pl. i, figs. 3 and 8) "Zeylon and Sina" (error).

1868. *Cadmus cuneiformis* Theobald, Cat. Rept. Asiatic Soc. Mus., p. 58: "Simla, India" (error).

1872. *Coronella phocarum* Günther, Proc. Zool. Soc. London, p. 836: Robben Island, Cape Province, South Africa.

1882. *Ophirhina Anchictae* Bocage, Jorn. Sci. Lisboa, **8**, p. 300: Caconda, Benguela, Angola.

Range. Uplands of Kenya Colony and Tanganyika Territory, south to Natal, west to the Cape, north through Southwest Africa to Angola east through southern Belgian Congo.

Genus **DUBERRIA** Fitzinger

1826. *Duberria* Fitzinger (part), Neue Class. Rept., pp. 29, 55. Type by tautonomy: *Coluber arctiventris* Daudin (1803) = *Coluber Duberria* Merrem (1790) = *Coluber lutrix* Linnaeus (1758).

1830. *Homalosoma* Wagler, Nat. Syst. Amphib., p. 190, footnote. Substitute name for *Duberria* Fitzinger.

1833. *Brachyblemma* Wagler, Isis von Oken, col. 904. Type by monotypy: *Coluber duberria* Merrem = *Coluber lutrix* Linnaeus.

Duberria lutrix abyssinica (Boulenger) Abyssinia Slug-eater

1894. *Homalosoma abyssinicum* Boulenger, Cat. Snakes Brit. Mus., **2**, p. 276, pl. xiii, fig. 2, Lake Ashanti, Ethiopia.

1912. *Homalosoma lutrix* var. *atriventris* Sternfeld, Wiss. Ergebn. Deut. Zentral-Afrika-Exped. 1907-1908, **4**, p. 271: "Kissenje," i.e. Kisenyi, Belgian Ruanda.

Range. Highlands of Ethiopia; Uganda; Kenya Colony and northern Tanganyika Territory,[123] west through Belgian Ruanda-Urundi to the Belgian Congo.

Duberria lutrix shirana (Boulenger) Shire Slug-eater

1894. *Homalosoma shiranum* Boulenger, Cat. Snakes Brit. Mus., **2**, p. 276, pl. xiii, fig. 1: Shire Highlands, Nyasaland.

Range. Highlands of southern Tanganyika Territory and Nyasaland.

Genus **GRAYIA** Günther

1857. *Heteronotus* Hallowell (not Laporte:1832), Proc. Acad. Nat. Sci. Philadelphia, p. 67. Type by monotypy: *Coronella triangularis* Hallowell = *Coluber smythii* Leach.

1858. *Grayia* Güuther, Cat. Snakes Brit. Mus., p. 50. Type by monotypy: *G. silurophaga* Günther = *Coluber smythii* Leach.

1862. *Glaniolestes* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 191. New name for *Heteronotus* Hallowell (preoccupied in Hemiptera).

1863. *Leionotus* Jan (not of Cocteau and Bibron:1843), Elenco Sist. Degli Ofidi, pp. 68, 74. Type by monotypy: *L. Schlegeli* Jan (based on ms. label *Tropidonotus glaber* in Leyden Museum).

1866. *Macrophis* Bocage, Jorn. Sci. Lisboa, **1**, p. 67. Type by monotypy: *M. ornatus* Bocage.

1863. *Xenurophis* Günther, Ann. Mag. Nat. Hist., (3) **12**, p. 357. Type by monotypy: *X. caesar* Günther.

Grayia smythii (Leach) Smyth's Water-Snake

1818. *Coluber Smythii* Leach, in Tuckey, Explor. River Zaire, App., p. 409: "Embomma," i.e. Boma, Belgian Congo.

1854. *Coronella triangularis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 100: Liberia.

1858. *Grayia silurophaga* Günther, Cat. Snakes Brit. Mus., p. 51: West Africa.

1863. *Lejonotus Schlegeli* Jan, Elenco Sist. Degli Ofidi, p. 74: Ashanti, Gold Coast.

Range. Rivers and lakes of Sudan and Uganda, southwest to Angola, north and west to Senegal.

Grayia tholloni Mocquard Tholloni's Water-Snake

1897. *Grayia Tholloni* Mocquard, Bull. Soc. Philom. Paris, (8) **9**, p. 11: French Congo.

[123] Though "Zanzibar" is included on a recent list, I cannot believe that this upland form (which occurs on Kilimanjaro and the Usambara Mountains) ever came from Zanzibar Island.

1901. *Grayia fasciata* Boulenger, Ann. Mus. Congo, (1) **2**, p. 9, pl. iii, fig. 3: Southwest of Lake Tanganyika, Belgian Congo.

Range. Rivers and lakes of Sudan; Uganda; western Kenya Colony and western Tanganyika Territory; west through the Belgian Congo to Angola.

Genus **BOIGA** Fitzinger[124]

1825. *Ibiba* Gray, Ann. Philos. (2), **10**, p. 209. Type by monotypy: *Coluber irregularis* Merrem.

1826. *Boiga* Fitzinger (part), Neue Class. Rept., pp. 29, 60. Type by subsequent designation: *Coluber irregularis* Merrem.

1843. *Dipsadomorphus* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Coluber trigonatus* Schneider.

1843. *Cephalophis* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Dipsas dendrophila* Boie.

1843. *Eudipsas* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Dipsas cynodon* Boie.

1843. *Macrocephalus* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Dipsas drapiczii* Boie.

1854. *Opetiodon* Duméril & Bibron, Erpét. Gén., **7**, p. 905. Type by monotypy: *Dipsas cynodon* Boie.

1854. *Triglyphodon* Duméril & Bibron, Erpét. Gén., **7**, p. 1069. Type by present designation: *Coluber irregularis* Merrem.

1857. *Toxicodryas* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 60. Type by monotypy: *Dipsas blandingii* Hallowell.

1877. *Pappophis* Macleay, Proc. Linn. Soc. N. S. Wales, **2**, p. 39. Type by monotypy: *P. laticeps* Macleay = *Coluber irregularis* Merrem.

1894. *Liophallus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 427. Type by original designation: *Dipsas fuscus* Gray.

Boiga blandingii (Hallowell) Blanding's Tree-Snake

1844. *Dipsas Blandingii* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 170: Liberia.

1854. *Triglyphodon fuscus* Duméril & Bibron, Erpét. Gén., **7**, p. 1101: Ivory Coast.

1856. *Dipsas fasciata* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 84, pl. iii, fig. 5: Peki, Gold Coast.

1856. *Dipsas valida* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 87, pl. iii, fig. 4: Edina, Grand Bassa County, Liberia.

[124] Together with *Geodipsas* (here placed near *Natriciteres*), the snakes from this point to the end of the COLUBRIDAE (except for an occasional *Aparallactus*) are backfanged. They constitute the OPISTHOGLYPHA of Boulenger, by whom they were placed in a subfamily known as the DIPSADOMORPHINAE (BOIGINAE of later authors), a group since discarded as unnatural because of independent derivation.

1856. *Dipsas globiceps* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 89, pl. iii, fig. 6: Edina, Grand Bassa County, Liberia.

1859. *Dipsas Fischeri* Jan (new name suggested by Jan to combine the three preceding age and color variations), in A. Duméril, Arch. Mus. Hist. Nat. (Paris), **10**, p. 212.

1871. *Dipsas regalis* "Schlegel" Jan, Icon. Gén. Ophid., livr. 38, note to pl. vi, fig. 2: Ivory Coast.

1885. *Dipsas globiceps* var. *tumboensis* F. Müller, Verh. Naturf. Ges. Basel, **7**, p. 688: Tumbo Island, French Guinea.

Range. Uganda, southwest through the Belgian Congo to Angola, northwest to French Guinea.[125]

Boiga pulverulenta (Fischer) Powdered Tree-Snake

1856. *Dipsas pulverulenta* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 81, pl. iii, fig. 1: Edina, Grand Bassa County, Liberia.

1917. *Dipsadomorphus Boueti* Chabanaud, Bull. Mus. Hist. Nat. (Paris), 1916, **22**, p. 373, figs. 13-15: Porto Novo, Dahomey.

Range. Uganda, southwest through the Belgian Congo to Angola, northwest to French Guinea.

Genus **DIPSADOBOA** Günther[126]

1858. *Dipsadoboa* Günther (part), Cat. Snakes Brit. Mus., p. 182. Type by subsequent restriction: *D. unicolor* Günther.

1869. *Anoplodipsas* Peters, Monatsb. Akad. Wiss. Berlin, p. 442. Type by monotypy: *A. viridis* Peters = *Dipsadoboa unicolor* Günther.

Dipsadoboa unicolor Günther Günther's Green Tree-Snake

1858. *Dipsadoboa unicolor* Günther, Cat. Snakes Brit. Mus., p. 183: West Africa.

1869. *Anoplodipsas viridis* Peters, Monatsb. Akad. Wiss. Berlin, p. 442, pl. —, fig. 4: "New Caledonia" (error).

1871. *Heterurus bicolor* Jan, Icon. Gén. Ophid., livr. 38, pl. ii, fig. 3: No locality.

1893. *Dipsadoboa assimilis* Matschie, Sitzb. Ges. Naturf. Freunde Berlin, p. 173: Bismarckburg, *i.e.*, Adele, Togo.

Range. Uganda, west through Belgian Congo to French

[125] Reported from Zanzibar in error by Boulenger (1896, Cat. Snakes Brit. Mus., **3**, p. 77) and consequently followed by many authors.

[126] For a key to the five species recognized by Laurent as of 1951, see Laurent, 1951, Revue Zool. Bot. Afr., **44**, p. 211. As of 31.xii.1956 I have not seen the description of the high-altitude *Dipsadoboa unicolor viridiventris* Laurent (mentioned by Curry-Lindahl, 1956, Ann. Mus. Royal Congo Belge, **42**, p. 45, as about to be published).

Guinea (but as yet unrecorded from Nigeria: Dahomey and Liberia).[127]

Genus **TELESCOPUS** Wagler

1830. *Telescopus* Wagler (not *Telescopium* Montfort:1810), Nat. Syst. Amphib., p. 182. Type by monotypy: *Coluber* on pl. v, figs. 11-13 in Savigny's Suppl. to Geoffroy, 1812, Descr. Egypte.

1831. *Tarbophis* F. L. Fleischmann, Dalm. Nov. Serp. Gen., p. 17. Type by monotypy (? as not seen): *T. fallax* Fleischmann.

1831. *Trigonophis* Eichwald, Zool. Spec. Rossiae Poloninae, Part 3, p. 175. Type by monotypy: *T. iberus* Eichwald.

1837. *Ailurophis* Bonaparte, Icon. Fauna Italica, **2**, Anfibi, p. 101. Type by monotypy: *Coluber vivax* Schreiber = *Tarbophis vivax* Duméril & Bibron.

1846. *Aelurophis* Agassiz, Nomen. Zool., Index Univers., p. 9. Emendation for *Ailurophis* Fitzinger = Bonaparte.

1935. *Migiurtinophis* Scortecci, Ann. Mus. Civ. Stor. Nat. Genova, **59**, p. 1. Type by monotypy: *M. pulcher* Scortecci.

Telescopus dhara somalicus (Parker)[128]

Southern Large-eyed Snake

1949. *Tarbophis dhara somalicus* Parker, Zool. Verh. Rijksmus. Nat. Hist. Leiden, No. 6, p. 88: Ngatana, Tana River, Kenya Colony.

Range. Southern Somalia and northern Kenya Colony.

Telescopus semiannulatus semiannulatus Smith

Eastern Tiger-Snake

1849. *Telescopus semiannulatus* A. Smith, Illus. Zool. S. Africa, Rept., pl. lxxii; South Africa (by inference).

1898. *Tarbophis semiannulatus* var. *meridionalis* Werner, Jahresb. Abhand. Naturw. Ver. Magdeburg, 1896-1897, p. 144: South Africa.

Range. Kenya Colony and Tanganyika Territory, south to Natal, northwest through Basutoland and Bechuanaland to

[127] Only represented in the Museum of Comparative Zoology by examples from Uganda, Belgian Congo and the French Cameroon; nor are there any specimens from west of the Cameroons in the British Museum as of today.

[128] The type from Ngatana was originally assigned by Boulenger (1896) to *Tarbophis guentheri* Anderson, considered by Parker to be synonymous with the typical form described as *Coluber dhara* Forskal (1775, Descr. Anim., p. 14). Probably the two Kenya records of *Tarbophis obtusus* Boettger (which is a synonym of *d. dhara*) from Njiri (? Nyeri or Uaso Nyiro) by Mocquard (1902), and from Lodwar by Parker (1936) are referable to *T. d. somalicus*. My own early (1916-1917) records from Gobwen (now Gobuin) and Kismayu (now Chisimaio) were made prior to the transfer of those places to what is now Somalia.

Southwest Africa (where it meets with a subspecies), north to Angola and the Belgian Congo.

Genus **CROTAPHOPELTIS** Fitzinger[129]

1843. *Crotaphopeltis* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Coronella rufescens* Schlegel = *Coronella hotamboeia* Laurenti.

1927. *Dipsoglyphophis* Barbour & Amaral, Bull. Antivenin Inst. America, **1**, p. 26. Type by original designation: *Leptodira guineensis* Chabanaud.

Crotaphopeltis werneri (Boulenger)[130]

1897. *Leptodira werneri* Boulenger, Ann. Mag. Nat. Hist., (6) **19**, p. 281: Usambara Mountains, Tanganyika Territory.

1909. *Dipsadomorphus reticulatus* Werner, Jahresb. Ver. Nat. Württemberg, **65**, p. 55: Tanga, Tanganyika Territory.

Range. Usambara Mountains and vicinity, Tanganyika Territory.

Crotaphopeltis hotamboeia kageleri Uthmöller

1939. *Crotaphopeltis hotamboeia kageleri* Uthmöller, Zool. Anz., **125**, p. 108: Sanya, Tanganyika Territory.

Range. Vicinity of Mount Kilimanjaro, Tanganyika Territory (known only from the types).

Crotaphopeltis hotamboeia tornieri (Werner)

Sylvicoline White-lipped Snake

1908. *Leptodira tornieri* Werner, 1907, Sitzb. Akad. Wiss. Wien, **116**, Abt. 1, p. 1876: Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of the Usambara and Uluguru Mountains, Tanganyika Territory, south to Misuku Mountains, northern Nyasaland.

Crotaphopeltis hotamboeia hotamboeia (Laurenti)

Savanna White-lipped Snake

1768. *Coronella hotamboeia* Laurenti, Syn. Rept., p. 85: "India orientali," i.e. Africa.

[129] The included species present gradual stages of habitus from the slender and attenuated arboreal forms like *C. duchesnii guineensis* to the moderately stout terrestrial *C. h. hotamboeia*. A revision of the entire complex of this genus in relation to *Telescopus, Dipsadoboa, Boiga* and their included species, together with a fresh evaluation of generic characters, is much needed. Piecemeal studies result only in inconclusive reshuffling of forms.

[130] I suspect that the record of *Dipsas obtusa* from Usambara (Werner:1895), repeated by Tornier (1896) was based on this specimen.

1768. *Coronella virginica* Laurenti, Syn. Rept., p. 86. No locality.
1789. *Coluber rufescens* Gmelin, Syst. Nat., ed. 13, **1**, Part 3, p. 1094 (based on Seba, Thesaurus, **1**, pl. xxxiii, fig. 6): No locality.
1833. *Coluber bicolor* Leach in Bowdich, Miss. Ashantee, p. 493: "Fantee," i.e. Fanti, Ashanti, Gold Coast.
1833. *Ophis Heterurus* Duvernoy, Ann. Sci. Nat. (Paris), **30**, p. 9, pl. i, fig. 2: No locality.
1843. *Dipsas hippocrepis* Reinhardt, Dansk. Vidensk. Selsk. Skrift, **10**, p. 251, pl. i, figs. 18-20: Guinea.
1849. *Dipsas inornatus* A. Smith, Illus. Zool. S. Africa, Rept. App., p. 20: Kaffirland eastward of Cape Colony, i.e. Natal.
1860. *Oxyropus melanocrotaphos* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 260: No locality.
1940. *Tarbophis barnumbrowni* Bogert, Bull. Amer. Mus. Nat. Hist., **77**, p. 66, fig. 9: Jigjiga, Ethiopia.

Range. Uganda; Kenya Colony; Tanganyika Territory; Zanzibar Island; indeed almost all Africa south of about 15° N. (though unrecorded from French and British Somaliland).

Crotaphopeltis degeni (Boulenger)[131]

1906. *Leptodira degeni* Boulenger, Proc. Zool. Soc. London, p. 572, fig. 97: Entebbe, Uganda.
1907. *Leptodira attarensis* Werner, Sitzb. Akad. Wiss. Wien, **116**, **1**, p. 1875, pl. iii, fig. 6: Sennar and Sobat, Sudan.

Range. Southern Sudan and Uganda.

Genus CHAMAETORTUS Günther

1864. *Chamaetortus* Günther, Proc. Zool. Soc. London, p. 310. Type by monotypy: *C. aulicus* Günther.

Chamaetortus aulicus aulicus Günther[132]

Cross-barred Tree-Snake

1864. *Chamaetortus aulicus* Günther, Proc. Zool. Soc. London, p. 310: Zambezi River.

Range. Kenya Colony; Tanganyika Territory and Zanzibar Island south through Mozambique.

[131] The relationship to *C. h. hotambocia* is obscure and a series is needed to demonstrate that they really can be distinguished.

[132] Trinomials are used as Mons. J. Guibé assures me (30.v.1956) that the young snake described in 1916 as *C. a. ellenbergeri* by Chabanaud appears to be correctly assigned. As its type locality "Lambaréné," Gabon, is well over 1500 miles from the nearest point where *aulicus* is known to occur, I suggest that there may be an error in the type locality, more especially as *Mabuya striata ellenbergeri* was taken by the same collector on the Zambezi at Lealui, Northern Rhodesia.

Genus **DISPHOLIDUS** Duvernoy

1829. *Bucephalus* A. Smith (not Baer:1827), Zool. Journ., **4**, p. 441. Type by monotypy (as other included species are synonyms): *B. typus* A. Smith.

1832. *Dispholidus* Duvernoy, Ann. Sci. Nat. (Paris), **26**, p. 150. Type by monotypy: *D. lalandii* Duvernoy = *Bucephalus typus* A. Smith.

1843. *Dryomedusa* Fitzinger, Syst. Rept., p. 26. Type by original designation: *Dendrophis colubrina* Schlegel = *Bucephalus typus* A. Smith.

Dispholidus typus (Smith) [133]

Boomslang or Back-fanged Tree-Snake

1829. *Bucephalus typus* A. Smith, Zool. Journ., **4**, p. 441: Old Latakoo, South Africa.[134]

1829. *Bucephalus jardinii* A. Smith, Zool. Journ., **4**, p. 442: South Africa.

1829. *Bucephalus gutturalis* A. Smith, Zool. Journ., **4**, p. 442: South Africa.

1829. *Bucephalus Bellii* A. Smith, Zool. Journ., **4**, p. 442: South Africa.

1832. *Dispholidus Lalandii* Duvernoy, Ann. Sci. Nat. (Paris), **26**, p. 150: Cape of Good Hope, i.e. South Africa.

1837. *Dendrophis colubrina* Schlegel, Essai Phys. Serp., **2**, p. 238, pl. ix, figs. 14-16: Rondebosch, Cape Province, South Africa.

1841. *Bucephalus viridis* A. Smith, Illus. Zool. S. Africa, Rept., pl. iii: Old Latakoo, South Africa.[134]

1841. *Bucephalus capensis* A. Smith, Illus. Zool. S. Africa, Rept., pls. x-xiii: Cape Province, South Africa.

1849. *Dendrophis pseudodipsas* Bianconi, 1848, Nuovi Ann. Sci. Nat., (2) **10**, p. 108, pl. iv, fig. 2; also 1850, Spec. Zool. Mosamb., p. 40, pl. iv, fig. 2: Mozambique.

[133] That six of the synonyms should have been described from South Africa by Sir Andrew Smith, bears testimony to the astonishing variation in color, due in part to differences of age or sex. I have personally taken four striking variants in, or near, a single avenue of trees at Morogoro, Tanganyika Territory. The all-black phase that occurs there, bears, both in color and scalation, so close a resemblance to the aglyphous *Thrasops jacksonii* that one wonders if descent, rather than convergence, is not the explanation.

The two races recently described by Laurent, are listed here because a paratype of one form comes from Tanganyika Territory. Possibly they are recognizable but their status requires to be studied in relation to the species as a whole, something I have not been able to do. The range of *typus*, as here understood, is as extensive as that of *Crotaphopeltis h. hotamboeia* and nearly as great as that of *Bitis a. arietans*, neither of which seems divisible to any appreciable extent.

[134] Old Latakoo, or Lattakoo as it was sometimes spelled in the early days, is more correctly rendered as Lithako. It was the principal kraal of the Batlaping tribe, approximately 27° S., 24° E., i.e. between Kuruman and Taungs, northern Cape Province.

1937. *Thrasops jacksonii mossambicus* Mertens, Abhand. Senckenberg. Naturf. Ges., No. 435, p. 13: Cheringoma Farm, Inhaminga, Mozambique.

1955. *?Dispholidus typus kivuensis* Laurent, Revue Zool. Bot. Afr., **51**, p. 127: ♂ from Uvira, 780 metres, Lake Tanganyika, Kivu District, Belgian Ruanda-Urundi.

1955. *?Dispholidus typus punctatus* Laurent, Revue Zool. Bot. Afr., **51**, p. 129: ♂ from Dundo, Angola.

Range. Uganda; Kenya Colony; Tanganyika Territory; Pemba, Zanzibar and Mafia Islands; indeed almost all Africa south of about 15° N. (though unrecorded from Dahomey; Sierra Leone and Gambia).

Genus **THELOTORNIS** Smith

1849. *Thelotornis* A. Smith, Illus. Zool. S. Africa, Rept., App. p. 19. Type by monotypy: *T. capensis* A. Smith.

1859. *Cladophis* A. Duméril, Arch. Mus. Hist. Nat. (Paris), **10**, p. 204. Type by monotypy: *Leptophis kirtlandii* Hallowell.

Thelotornis kirtlandii kirtlandii (Hallowell) Northern Vine-Snake[135]

1844. *Leptophis Kirtlandii* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 62: Liberia.

1854. *Oxybelis Lecomtei* Duméril & Bibron, Erpét. Gén., **7**, p. 821: Gabon, French Congo.

1854. *Tragops rufulus* Duméril & Bibron, Erpét. Gén., **7**, p. 827: Senegal.

1856. *Oxybelis violacea* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 91, pl. ii, fig. 7: Edina, Grand Bassa County, Liberia.

Range. Somalia, south through Uganda and Kenya Colony to northern Tanganyika Territory (where it meets and merges with the southern race) southwest to central Angola, north and west to Portuguese Guinea.

Thelotornis kirtlandii capensis Smith Southern Vine-Snake

1849. *Thelotornis capensis* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 19: Kaffirland and the country towards Port Natal, i.e. Durban, Natal.

1895. *Thelotornis Kirtlandii* var. *mossambicana* Bocage, Herp. Angola Congo, p. 119: Manica, Mozambique (restricted).

Range. Southern Tanganyika Territory and Mafia Island.

[135] A name slightly preferable to Bird-Snake, for, though its principal prey may consist of birds and nestlings at certain seasons or in some localities, elsewhere chameleons and other reptiles figure largely in its menu.

south (except in area occupied by *T. k. oatesii* Günther) to Natal, northwest to northern Southwest Africa and southern Angola (where it meets and merges with the northern race).

Genus **HEMIRHAGERRHIS** Boettger[136]

1893. *Hemirhagerrhis* Boettger, Zool. Anz., **16**, p. 129. Type by monotypy: *H. kelleri* Boettger.

Hemirhagerrhis kelleri Boettger Stripe-bellied Snake

1893. *Hemirhagerrhis kelleri* Boettger, Zool. Anz., **16**, p. 129: "Abdallah," i.e. Abdulla, north of Webi Shebeli, Ethiopia.

1908. *Amplorhinus taeniatus* Sternfeld, Mitt. Zool. Mus. Berlin, **4**, p. 244, fig. 3: Lamu Island, Kenya Colony.

Range. Ethiopia and British Somaliland, south through Somalia to Mombasa and Voi, Kenya Colony.

Hemirhagerrhis nototaenia nototaenia (Günther) Eastern Spot-striped Snake

1864. *Coronella nototaenia* Günther, Proc. Zool. Soc. London, p. 309, pl. xxvi, fig. 1: Rios de Sena, Zambezi, Mozambique.

1878. *Ablabes Hildebrandtii* Peters, Monatsb. Akad. Wiss. Berlin, p. 205, pl. ii, fig. 6: Kitui, Ukamba, Kenya Colony.

1905. *Amplorhinus Güntheri* Mocquard, Bull. Mus. Hist. Nat. (Paris), **12**, p. 251: Lake Ngami, Bechuanaland Protectorate.

Range. Sudan and British Somaliland south through Kenya Colony and Tanganyika Territory to Mozambique and Bechuanaland, north through the Rhodesias to Belgian Congo.

Genus **PSAMMOPHYLAX** Fitzinger[137]

1768. *Cerastes* Laurenti, Syn. Rept., p. 81. Type by subsequent designation of Fejérváry:1923: *Coluber rhombeatus* Linnaeus. Type by subsequent designation of Stejneger:1936: *Cerastes candidus* Laurenti = *Coluber haje* Linnaeus, i.e. *Naja haje* (Linnaeus).

[136] Bogert (1940, Bull. Amer. Mus. Nat. Hist., **77**, p. 75) considers *Amplorhinus* A. Smith (1847, Ill. Zool. S. Africa, Rept., text to pl. lvii) must for the present be regarded as a monotypic genus, with *A. multimaculatus* Smith the only species.

[137] Technically *Cerastes* is correct, but in view of its application to the horned vipers of North Africa for so long (I have over 160 citations in this sense between 1880 and 1950), to use it for the more or less innocuous opisthoglyphous grass-snakes of East and South Africa seems to imply a pedantic devotion to legality. In view of the medical implications involved in anti-cerastes serum and the frequency with which the name *Cerastes* has appeared in medical literature, it should be rejected, or Stejneger's solution of the difficulty accepted.

1843. *Psammophylax* Fitzinger, Syst. Rept., p. 26. Type by original designation: *Coluber rhombeatus* Linnaeus.

1847. *Trimerorhinus* A. Smith, Illus. Zool. S. Africa, Rept., text to pl. lvi. Type by monotypy: *Coluber rhombeatus* Linnaeus.

Psammophylax tritaeniatus multisquamis (Loveridge)[138]

Many-scaled Grass-Snake

1932. *Trimerorhinus tritaeniatus multisquamis* Loveridge, Proc. Biol. Soc. Washington, **45**, p. 84: Nairobi, Kenya Colony.

Range. Highlands of Ethiopia and Kenya Colony, south (in highlands) to the Central Railway, Tanganyika Territory.

Psammophylax tritaeniatus variabilis Günther[139]

Gray-bellied Grass-Snake

1893. *Psammophylax variabilis* Günther, Proc. Zool. Soc. London, 1892, p. 557, col. pl. xxxv: Shire Highlands, Nyasaland.

Range. Highlands of Tanganyika Territory (south of the Central Railway), south (in highlands) to Mozambique and Nyasaland.

Psammophylax tritaeniatus tritaeniatus (Günther)

White-bellied Grass-Snake

1868. *Rhagerrhis tritaeniatus* Günther, Ann. Mag. Nat. Hist., (4) **1**, p. 423, pl. xix, fig. H: Southeastern Africa.

1881. *Coronella tritaenia* Günther, in Frank Oates, Matabeleland and the Victoria Falls (London), App. 3, p. 329, pl. C: "Southeastern Africa," i.e. Matabeleland, Southern Rhodesia.

Range. Dry savanna of Tanganyika Territory, south to Natal, west to Southwest Africa, north to Angola, east through southern Belgian Congo to Lake Tanganyika.

Genus **RHAMPHIOPHIS** Peters

1854. *Rhamphiophis* Peters, Monatsb, Akad. Wiss. Berlin, p. 624. Type by monotypy: *R. rostratus* Peters.

1863. *Dipsina* Jan, Arch. Zool. Anat. Fisiol., **2**, pp. 215, 313. Type by monotypy: *Coronella multimaculata* A. Smith.

[138] Early Kenya and Tanganyika records appeared as *Rhagerrhis tritaeniata*; my own first captures were erroneously recorded as *Psammophis brevirostris*. Boulenger's (1896:649) record of *Trimerorhinus tritaeniatus* from "Uganda," like others from the same source, should read Kenya Colony.

[139] The *"Trimerorhinus rhombeatus"* record of Sternfeld (1910) from Ukinga, southern Tanganyika Territory, was almost certainly based on a misidentified *P. t. variabilis*, the form which is abundant throughout the southern highlands.

Rhamphiophis acutus acutus (Günther)
Southern Striped Beaked-Snake

1888. *Psammophis acutus* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 327, pl. xix, fig. D: Pungo Ndongo, Angola.

Range. Southern Tanganyika Territory west through Northern Rhodesia to Angola, northeast through the Belgian Congo to Belgian Ruanda-Urundi.

Rhamphiophis rubropunctatus (Fischer)
Red-spotted Beaked-Snake

1884. *Dipsina rubropunctata* Fischer, Jahrb. Hamburg. Wiss. Anst., **1**, p. 7, pl. i, fig. 3: Near Arusha, Tanganyika Territory.

Range. Sudan east to British Somaliland, south through Somalia and eastern Kenya Colony to northeastern Tanganyika Territory, and (*fide* Moreau and Pakenham) Zanzibar Island.

Rhamphiophis oxyrhynchus rostratus Peters
Eastern Brown Beaked-Snake

1854. *Rhamphiophis rostratus* Peters, Monatsb. Akad. Wiss. Berlin, p. 624: Tete; Mesuril and Quitangonha, Mozambique.

1868. *Rhagerrhis unguiculata* Günther, Ann. Mag. Nat. Hist., (4) **1**, p. 422, pl. xix, fig. G: Zanzibar.

1870. *Coelopeltis porrectus* Jan, Icon. Gén. Ophid., livr. 34, pl. ii, fig. 1: Africa?

Range. Sudan east to Somalia, south through Kenya Colony; Tanganyika Territory and Zanzibar Island to Mozambique, west through Nyasaland and Northern Rhodesia to southeastern Belgian Congo.

Rhamphiophis oxyrhynchus oxyrhnchus (Reinhardt)
Western Brown Beaked-Snake

1843. *Psammophis oxyrhynchus* Reinhardt, Dansk. Vidensk. Selsk. Skrift., **10**, p. 244, pl. i, figs. 10-12: Guinea.

1929. *Rhamphiophis connali* Parker, Ann. Mag. Nat. Hist., (10) **4**, p. 450: Accra, Gold Coast.

Range. Uganda, west through northern Belgian Congo to Nigeria; Togo; Gold Coast; French Soudan.

Genus **DROMOPHIS** Peters[140]

1843. *Philodendros* Fitzinger, Syst. Rept., p. 26. Type by original

[140] Unfortunately this name is antedated by *Philodendros*, a most misleading name for a terrestrial snake that bears a strong resemblance to *Psammophis*. The sooner a ruling to reject *Philodendros* can be obtained, the better.

designation: *Dendrophis praeornata* Schlegel.

1846. *Philodendrus* Agassiz, Nomen. Zool., Index Univers., p. 285. Emendation for *Philodendros* Fitzinger.

1869. *Dromophis* Peters, Monatsb. Akad. Wiss. Berlin, p. 447. Type by monotypy: *Dendrophis praeornata* Schlegel.

Dromophis lineatus (Duméril & Bibron)

Buff-striped Grass-Snake

1854. *Dryophylax lineatus* Duméril & Bibron, Erpét. Gén., **7**, p. 1124: White Nile, Sudan.

1901. *Psammophis sibilans tumbensis* Schenkel, Verh. Naturf. Ges. Basel, **13**, p. 172: Tumbo Island, French Guinea.

1902. *Psammophis brevirostris temporalis* Werner, Verh. Zool. Bot. Ges. Wien, **52**, p. 335: Coja, Togo.

Range. Sudan and Uganda, south along Lake Tanganyika, Tanganyika Territory to northern Nyasaland and Northern Rhodesia, northwest through the Belgian Congo to Portuguese Guinea (though as yet not recorded from the Gold Coast and Sierra Leone).

Genus **PSAMMOPHIS** Boie[141]

1819. *Macrosoma Leach* (not Hübner:1818), in Bowdich, Miss. Ashantee, App., p. 493. Type by monotypy: *Coluber elegans* Shaw.

1826. *Psammophis* Boie, Isis von Oken, **19**, col. 982. Type by monotypy: *Coluber sibilans* Linnaeus.

1826. *Psammophis* Fitzinger, Neue Class. Rept., pp. 29, 30. Type according to Boie: *Coluber sibilans* Linnaeus.

1827. *Psammophis* Boie (part), Isis von Oken, **20**, col. 521. Type by specific designation: *Coluber sibilans* Linnaeus.

1838. *Taphrometopon* Brandt, Bull. Acad. Sci. St. Petersburg, **3**, p. 243. Type by monotypy: *Coluber* (*T.*) *lineolatus* Brandt.

1854. *Chorisodon* Duméril & Bibron, Erpét. Gén., **7**, p. 901. Type by monotypy: *C. sibiricum* Duméril & Bibron = *Coluber lineolatus* Brandt.

1854. *Monodiastema* G. Bibron, in Duméril & Bibron, Erpét. Gén., **7**, p. 901. Type by monotypy: *Chorisodon sibericum* Duméril & Bibron = *Coluber* (*Taphrometopon*) *lineolatus* Brandt.

1868. *Phayrea* Theobald, Cat. Rept. Asiatic Soc. Mus., p. 51. Type by monotypy: *P. isabellina* Theobald = *Coluber condanarus* Merrem.

[141] Owing to some confusion as to authorship I have cited all three of the earliest records; Fitzinger attributes the name to Boie.

1872. *Amphiophis* Bocage, Jorn. Sci. Lisboa, **4**, p. 81. Type by monotypy: *A. angolensis* Bocage.

1892. *Rhamphophis* Boulenger, Zool. Rec. for 1891, p. 12. New name for *Amphiophis* Bocage, preoccupied.

1924. *Mike* Werner, Sitzb. Akad. Wiss. Wien, **133**, Abt. 1, p. 51. Type by monotypy: *M. elegantissimus* Werner = *Coluber condanarus* Merrem.

Psammophis punctulatus trivirgatus Peters

Southern Speckled Sand-Snake

1878. *Psammophis punctulatus* var. *trivirgatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 206 "Taita," i.e. Teita, Kenya Colony.

Range. British Somaliland and Somalia, south through Uganda (?) and Kenya Colony to Arusha and Same, Tanganyika Territory.

Psammophis sibilans sibilans (Linnaeus) Hissing Sand-Snake

1758. *Coluber sibilans* Linnaeus (part), Syst. Nat., ed. 10, **1**, p. 222: "Asia," (error).

1802. *Coluber Gemmatus* Shaw, Gen. Zool., **3**, p. 535: No locality.

1803. *Coluber moniliger* Daudin, Hist. Nat. Rept., **7**, p. 69: No locality.

1827. *Coluber auritus* Geoffroy Saint-Hilaire, Rept., in Descr. Égypte, pp. 147, 151, pl. viii, fig. 4: Egypt.

1856. *Psammophis irregularis* Fischer, Abhand. Nat. Ver. Hamburg, **3**, p. 92: Peki, Gold Coast.

1881. *Psammophis brevirostris* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 89: Xa-Matlale, Mozambique.

1882. *Psammophis sibilans* var. *mossambica* Peters, Reise nach Mossambique, **3**, p. 122: Mozambique Island, Mozambique.

1882. *Psammophis sibilans* var. *tettensis* Peters, Reise nach Mossambique, **3**, p. 122: Tete and Mozambique Island, Mozambique.

1884. *Psammophis sibilans* var. *intermedius* Fischer, Jahrb. Hamburg. Wiss. Anst., **1**, p. 14: Arusha, Tanganyika Territory.

1887. *Psammophis sibilans* var. *leopardinus* Bocage, Jorn. Sci. Lisboa, **11**, p. 206: Catumbela and interior Mossamedes, Angola.

1908. *Psammophis thomasi* Gough, Ann. Transvaal Mus., **1**, p. 30, fig. —: Salisbury, Southern Rhodesia.

Range. In suitable savanna country from Egypt south through Uganda; Kenya Colony; Tanganyika Territory and Zanzibar Island to Natal; northwest to Southwest Africa and on to Mauretania (outside of forested areas occupied by *P. s. phillipsii*); east to the Sudan.

Psammophis subtaeniatus sudanensis Werner

Northern Stripe-bellied Sand-Snake

1919. *Psammophis subtaeniatus* var. *sudanensis* Werner, Denks. Akad. Wiss. Wien, **96**, p. 504: Kadugli, Sudan.

Range. Drier regions of the southern Sudan and southern Ethiopia, south through Uganda; Kenya Colony; Tanganyika Territory; Zanzibar and Mafia Islands, to northern Mozambique and Nyasaland.[142]

Psammophis biseriatus tanganicus Loveridge

Western Link-marked Sand-Snake

1940. *Psammophis biseriatus tanganicus* Loveridge, Bull. Mus. Comp. Zool., **87**, p. 57: Mangasini, Usandawi, Tanganyika Territory.

Range. Southern Libya, southeast through the Sudan to Eritrea, British Somaliland and Ethiopia (where it meets with *P. b. biseriatus* along the Ethiopian-Somali border north of the Nogal River); south through Uganda to western Tanganyika Territory.

Psammophis biseriatus biseriatus Peters

Eastern Link-marked Sand-Snake

1881. *Psammophis biseriatus* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 88: "Taita," i.e. Teita, Kenya Colony.

1913. *Psammophis bitaeniatus* (lapsus for *biseriatus*) Boettger, in Voeltzkow, Reise in Ost-Afrika, **3**, p. 355: Patta Island, Kenya Colony.

Range. Somalia, south through eastern Kenya Colony to northeastern Tanganyika Territory (where it meets with *P. b. tanganicus* in the vicinity of Lake Manka).

Psammophis angolensis (Bocage) Pigmy Sand-Snake

1872. *Amphiophis angolensis* Bocage, Jorn. Sci. Lisboa, **4**, p. 82: Dondo, Cuanza River, Angola.

1877. *Ablabes Homeyeri* Peters, Monatsb. Akad. Wiss. Berlin, p. 620: Pungo Ndongo, Angola.

Range. Tanganyika Territory and Zanzibar Island, south to Mozambique, west through Nyasaland and Northern Rhodesia to Angola and the Belgian Congo.

[142] The typical form *P. s. subtaeniatus* Peters (with its synonyms *P. moniliger* var. *bilineatus* Peters:1867; *P. bocagii* Boulenger:1895; and *P. transvaalensis* Gough:1908), characterized by *three* labials entering the orbit, occurs in central Mozambique and extends right across southern Africa south of the Zambezi.

Genus **CALAMELAPS** Günther[143]

1849. *Choristodon* A. Smith (not Jonas:1844), Illus. Zool. S. Africa, Rept., App., p. 18: Type by monotypy: *C. concolor* Smith.

1866. *Calamelaps* Günther, Ann. Mag. Nat. Hist., (3) **18**, p. 26. Type by original designation: *Calamaria unicolor* Reinhardt.

1947. *Choristocalamus* Witte & Laurent, Mem. Mus. Hist. Nat. Belgique, 29, p. 16. New name for *Choristodon* Smith (preoccupied).

Calamelaps unicolor unicolor (Reinhardt)[144]

Seventeen-scaled Purple-Glossed Snake

1843. *Calamaria unicolor* Reinhardt, Dansk. Vidensk. Selsk. Skrift., **10**, p. 236, pl. i, figs. 1-3: Guinea.

1877. *Atractaspis Hildebrandtii* Peters, Monatsb. Akad. Wiss. Berlin, p. 616, pl. —, fig. 3: Zanzibar Coast, i.e. Tanganyika Territory.

1923. *Calamelaps niangarae* Schmidt, Bull. Amer. Mus. Nat. Hist., **49**, p. 117, fig. 12: Niangara, Belgian Congo.

Range. Uganda; Kenya Colony and Tanganyika Territory, west to Sierra Leone.

Calamelaps unicolor warreni Boulenger

Nineteen-scaled Purple-glossed Snake

1908. *Calamelaps warreni* Boulenger, Ann. Natal Mus., **1**, pp. 230, 234, fig. 3: Kosi Bay, Zululand.

1915. *Calamelaps mellandi* Boulenger, Proc. Zool. Soc. London, p. 214: Chirini Island, Lake Bangweulu, Northern Rhodesia.

Range. Kenya Colony and Tanganyika Territory, south through Mozambique and the Rhodesias to the Transvaal and Zululand, Natal.

Calamelaps unicolor polylepis Bocage

Twenty-one scaled Purple-glossed Snake

1873. *Calamelaps polylepis* Bocage, Jorn. Sci. Lisboa, **4**, p. 216: Dondo, Cuanza River, Angola.

[143] Under the name of *Choristocalamus*, Witte and Laurent (*loc. cit.*) would revive Smith's monotypic genus *Choristodon* on the grounds that it has retained an anterior temporal, a seventh upper labial, and posterior sublinguals — characters that seem inadequate to me.

On the other hand their action in synonymizing *Rhinocalamus* with *Calamelaps* has much to commend it, but the genotype — which is the only species known to me — occupies so intermediate a position in relation to certain other genera that I have preferred to retain it until further work has been done on the group.

[144] Only 17-scaled snakes occur in West Africa north of the Equator; in the east they appear to be associated with the surviving montane or gallery forests, but occasional individuals (about one in twenty) occur at Liwale in southeastern Tanganyika Territory where 19-scaled specimens predominate. For these the name *C. u. warreni* is retained — at least until its distribution is worked out in relation to that of *C. u. polylepis* which appears to have only 21 scales in Angola.

1888. *Calamelaps miolepis* Günther, Anu. Mag. Nat. Hist., (6) **1**, p. 323: Cape Maclear, Lake Nyasa, Nyasaland.

Range. Tanganyika Territory (*fide* a single old record from Tukuyu), south to Nyasaland; Southern Rhodesia; Angola.

Genus **RHINOCALAMUS** Günther

1888. *Rhinocalamus* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 322. Type by monotypy: *R. dimidiatus* Günther.

Rhinocalamus dimidiatus Günther

1888. *Rhinocalamus dimidiatus* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 322, pl. xix, fig. C: Mpwapwa, Ugogo, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type locality).

Genus **MICRELAPS** Boettger

1880. *Micrelaps* Boettger, Ber. Senckenberg. Naturf. Ges., p. 136. Type by monotypy: *M. mülleri* Boettger.

1888. *Elaposchema* Mocquard, Mem. Cent. Soc. Philom. Paris, p. 122. Type by monotypy: *E. vaillanti* Mocquard.

Micrelaps bicoloratus Sternfeld

1908. *Micrelaps bicoloratus* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 93: Kibwezi, Kenya Colony.

1908. *Rhinocalamus melcagris* Sternfeld, Mitt. Zool. Mus. Berlin, **4**, p. 244, fig. 4: Lamu Island, Kenya Colony.

Range. Kenya Colony and Tanganyika Territory (N.E. of Lake Manyara).

Genus **AMBLYODIPSAS** Peters

1856. *Amblyodipsas* Peters, Monatsb. Akad. Wiss. Berlin, p. 592. Type by monotypy: *Calamaria microphthalma* Bianconi.

Amblyodipsas katangensis ionidesi Loveridge

1951. *Amblyodipsas katangensis ionidesi* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 193: Tunduru, Southern Province, Tanganyika Territory.

Range. Tanganyika Territory.

Genus **MIODON** Duméril[145]

1858. *Microsoma* Jan (not Macquart:1855), Revue Mag. Zool., (2) **10**, p. 519. Type by monotypy: *M. neuwiedii* Jan.

1859. *Miodon* A. Duméril, Arch. Mus. Hist. Nat. (Paris), **10**, p. 206. Type by monotypy: *Elapomorphus gabonensis* A. Duméril.

1860. *Urobelus* Reinhardt, Vidensk. Meddel, Kjøbenhavn, p. 229. Type by monotypy: *U. acanthias* Reinhardt.

1902. *Cynodontophis* Werner, Verh. Zool. Bot. Ges. Wien, **52**, p. 346. Type by monotypy: *C. aemulans* Werner = *Microsoma notatum* Peters.

1941. *Melanocalamus* Witte, Explor. Parc. Nat. Albert, Miss. G. F. de Witte, Fasc. 33, p. 216. Type by monotypy: *M. leopoldi* Witte.

Miodon collaris collaris (Peters) Pale-collared Snake-eater

1881. *Microsoma collare* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 148: Macange, "Cuango" i.e. Kwango, French Congo.

1887. *Microsoma fulvicollis* Mocquard, Bull. Soc. Philom. Paris, (7) **11**, p. 65: Franceville, French Congo.

1888. *Elapomorphus caeutiens* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 323, pl. xix, fig. B: Cameroon Mountain, British Cameroon.

1910. *Cynodontophis werneri* L. Müller, Abhand. Bayer Akad. Wiss., 2 Kl., **24**, p. 612: Cameroon.

Range. Southwestern Uganda, west to Cameroon and possibly Nigeria.

Miodon collaris christyi Boulenger Eastern Snake-eater

1903. *Miodon Christyi* Boulenger, Ann. Mag. Nat. Hist., (7) **12**, p. 354: Uganda.

1923. *Miodon unicolor* Schmidt, Bull. Amer. Mus. Nat. Hist., **49**, p. 119, fig. 13: Poko, Belgian Congo.

Range. Central Uganda, south to western Tanganyika Territory, west to eastern Belgian Congo.

[145] It is impossible at this time to investigate the numerous changes proposed by Witte and Laurent (1947, Mem. Mus. Roy. Hist. Nat., 29, pp. 58-89) but two ♂♂ *gabonensis* (M.C.Z. 49727, 53737) from the Gold Coast (which they would perhaps assign to *neuwiedi* Jan) have 218 and 233 ventrals respectively, while two ♀♀ (M.C.Z. 53738, etc.) have 247 and 259. This would appear to effectively dispose of the alleged race *M. g. schmidti* Witte and Laurent from the Congo. On zoogeographical grounds, together with size and color pattern, I accept their separation of *gabonensis* from the *collaris* group, but not on the basis of adult eye diameter — being at least twice its distance from the mouth in *gabonensis*, as opposed to less than twice its distance in *collaris*, *fulvicollis*, etc. Our material fails to support this allegation for the first two *collaris* — taken at random — had eye diameters that were included 1½ (M.C.Z. 42956:Congo) to 2 or rather more than 2 times (M.C.Z. 9254:Cameroon) their distance from the border of the mouth — a very poor character indeed.

Miodon collaris graueri Sternfeld

Central-Lake-Region Snake-eater

1908. *Miodon Graueri* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 94: "Entetbe," i.e. Entebbe, Uganda.[146]

Range. Central Uganda, southwest to eastern Belgian Congo (L. Kivu).

Genus **CHILORHINOPHIS** Werner[147]

1907. *Chilorhinophis* Werner, Akad. Anz. Wien, **44**, p. 479 (brief notice) and 1908 (for 1907), Sitzb. Akad. Wiss. Wien, **116**, Abt. 1, p. 1881. Type by monotypy: *C. butleri* Werner.

1927. *Parkerophis* Barbour & Amaral, Bull. Antivenin Inst. America, **1**, p. 25. Type by original designation: *Apostolepis gerardi* Boulenger.

Chilorhinophis gerardi tanganyikae Loveridge

Tanganyika Two-headed Snake

1951. *Chilorhinophis gerardi tanganyikae* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 195: Nyamkolo, Lake Tanganyika, Northern Rhodesia.

Range. Western Tanganyika Territory (Ujiji), south to Northern Rhodesia (Nyamkolo), west to southern Belgian Congo (Lukonzolwa).

Chilorhinophis carpenteri liwalensis Loveridge

Liwale Two-headed Snake

1951. *Chilorhinophis carpenteri liwalensis* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 196: Liwale, Southern Province, Tanganyika Territory.

Range. Southeastern Tanganyika Territory.

Genus **APARALLACTUS** Smith

1849. *Aparallactus* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 15. Type by monotypy: *A. capensis* Smith.

1849. *Elapomorphus* A. Smith (not of Wiegmann: in Fitzinger:1843).

[146] Entebbe may be viewed with suspicion for Capt. C. R. S. Pitman, who resided at Entebbe for many years, failed to find it there and doubts its occurrence. Allegedly Grauer, like some other collectors, failed to label his material immediately. The nearest point to Entebbe from which the Museum of Comparative Zoology has *c. graueri*, is Kingani, 5000 feet, near Fort Portal (M.C.Z. 54737: coll. J. H. Blower, Esq. xi.1955).

[147] The Amani, Usambara Mountains, record of the Sudanese *butleri* is believed to have been based on a misidentification, possibly of an *Aparallactus werneri*.

Illus. Zool. S. Africa, Rept., App. p. 16, footnote. Type by monotypy: *E. capensis* Smith.

1854. *Uriechis* Peters, Monatsb. Akad. Wiss. Berlin, p. 623. Type by subsequent designation: *U. lunulatus* Peters.

1859. *Elapops* Günther, Ann. Mag. Nat. Hist., (3) **4**, p. 161. Type by monotypy: *E. modestus* Günther.

1860. *Periaspis* Cope, Proc. Acad. Nat. Sci. Philadelphia, pp. 241, 266. Type by monotypy: *P. plumbeatra* Cope = *Elapops modestus* Günther.

1863. *Cercocalamus* Günther, Ann. Mag. Nat. Hist., (3) **11**, p. 21. Type by monotypy: *C. collaris* Günther = *Aparallactus capensis* Smith.

1870. *Metopophis* Peters, Monatsb. Akad. Wiss. Berlin, p. 643, pl. i, fig. 3. Type by monotypy: *Uriechis lineatus* Peters.

1917. *Roulcophis* Chabanaud, Bull. Mus. Hist. Nat. (Paris), 1916, **22**, p. 379. Type by monotypy: *R. chevalieri* Chabanaud = *Uriechis lineatus* Peters.

1923. *Guyomarchia* Angel, Bull. Mus. Hist. Nat. (Paris), **29**, p. 348. Type by monotypy: *G. unicolor* Angel = *Elapops modestus* Günther.

Aparallactus modestus (Günther)[148]

Western-Forest Centipede-eater

1859. *Elapops modestus* Günther, Ann. Mag. Nat. Hist., (3) **4**, p. 161, pl. iv, fig. C: West Africa.

1860. *Periaspis plumbeatra* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 242: Liberia.

1896. *Aparallactus boulengeri* Werner, Verh. Zool. Bot. Ges. Wien, **46**, p. 363, pl. vi, figs. 6-6b: Cameroon.

1897. *Aparallactus peraffinis* Werner, Verh. Zool. Bot. Ges. Wien, **47**, p. 404, pl. ii, fig. 3: Interior of Cameroon.

1897. *Aparallactus ubangensis* Boulenger, Ann. Mag. Nat. Hist., (6) **19**, p. 279, fig. —: Zongo, Ubangi Rapids, Belgian Congo.

1901. *Aparallactus flavitorques* Boulenger, Ann. Mus. Congo, (1) **2**, p. 11, pl. iv, fig. 3: Lubué, Kasai, Belgian Congo.

[148] Material of *modestus* in the Museum of Comparative Zoology lends no support whatever to the action of Witte and Laurent (1947, pp. 99, 103) in reviving *ubangensis* as a race of *modestus*, to whose synonymy I had relegated it in 1944 (p. 187). The lower labials do not conform to their key and, taken from East to West we find the parietal is in contact with the 5th upper labial only (1 side) or 5th and 6th (5 sides) or 6th upper labial (2 sides) in Uganda snakes.
5th only (2 sides) on a ♂ (M.C.Z. 53994) from Mayala, B. C.
parietal in contact with 6th upper labial (M.C.Z. 42944) at Makaia, B. C.
5th and 6th (4 ex.) or 6th upper labial (2 ex.) at Bitye, F. C.
5th and 6th (1 ex.) at Accra, G. C.
5th and 6th (1 ex.), or 6th upper labial (1 ex.) in Liberia.
In other words, both *m. modestus* and *m. ubangensis* occur in Liberia; Gold Coast (or possibly not *m. modestus*); French Cameroon; Belgian Congo and Uganda.

1902. *Aparallactus dolloi* Werner, Verh. Zool. Bot. Ges. Wien, **52**, p. 346: Banzyville, Ubangi River, Belgian Congo.

1902. *Aparallactus congicus* Werner, Verh. Zool. Bot. Ges. Wien, **52**, p. 346: Lingunda, Belgian Congo.

1907. *Aparallactus Batesii* Boulenger, Ann. Mag. Nat. Hist., (7) **19**, p. 325: 5 miles inland from Kribi, French Cameroon.

1910. *Aparallactus Christyi* Boulenger, Ann. Mag. Nat. Hist., (8) **5**, p. 512: Mabira Forest, "Chagwe," i.e. Kyagwe, Uganda.

1917. *Aparallactus nigrocollaris* Chabanaud, Bull. Mus. Hist. Nat. (Paris), 1916, **22**, p. 377, figs. 18-19: French Congo.

1917. *Aparallactus nigrocollaris Roucheti* Chabanaud, Bull. Mus. Hist. Nat. (Paris), 1916, **22**, p. 378, figs. 20-21: French Congo.

1923. *Guyomarchia unicolor* Angel, Bull. Mus. Hist. Nat. (Paris), **29**, p. 348, figs. 1-4: (probably near Sangha) French Congo.

1924. *Aparallactus Graueri* Werner, Sitzb. Akad. Wiss. Wien, **133**, Abt. 1, p. 42: Beni, Belgian Congo.

Range. Uganda, west to Sierra Leone.

Aparallactus lunulatus lunulatus (Peters)

Southeastern Plumbeous Centipede-eater

1854. *Uriechis lunulatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 623: Tete, Mozambique.

Range. Sudan and Belgian Congo, south to Uganda (Mt. Rom) and Tanganyika Territory; Mozambique; Nyasaland; the Rhodesias and Transvaal.

Aparallactus lunulatus concolor (Fischer)

Northeastern Plumbeous Centipede-eater

1884. *Uriechis concolor* Fischer, Jahrb. Hamburg. Wiss. Anst., **1**, p. 4, pl. i, fig. 1: Arusha, Tanganyika Territory.

1931. *Aparallactus concolor boulengeri* Scortecci (not Werner:1896), Atti. Soc. Sci. Nat. Ital. (Milano), **70**, p. 212: Villaggio Duca degli Abruzzi and inland from Mogadiscio, Somalia.

Range. Sudan, east to Eritrea, south through eastern Kenya Colony to northern Tanganyika Territory.

Aparallactus jacksonii jacksonii (Günther)

Kilimanjaro Centipede-eater

1888. *Uriechis Jacksonii* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 325, pl. xix, fig. E: Foot of Mount Kilimanjaro, Tanganyika Territory.

Range. Southern Ethiopia, south through Kenya Colony to Tanganyika Territory.[149]

[149] A race (*A. j. oweni* Loveridge) occurs at Torit in the southern Sudan.

Aparallactus werneri Boulenger Usambara Centipede-eater

1895. *Aparallactus Werneri* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 172: Usambara Mountains, Tanganyika Territory.

Range. Eastern Tanganyika Territory.

Aparallactus turneri Loveridge Malindi Centipede-eater

1935. *Aparallactus turneri* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 9: Sokoki Forest, near Malindi, Kenya Colony.

Range. Coastal Kenya Colony (from Lamu to Mombasa).

Aparallactus guentheri Boulenger[150] Zanzibar Centipede-eater

1895. *Aparallactus guentheri* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 172: "East and Central Africa" (omit Angola). Subsequently types were designated as from Zanzibar; Shire Highlands and Lake Nyasa, Nyasaland.

1928. *Aparallactus uluguruensis* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 132: Nyange, Uluguru Mountains, Tanganyika Territory.

Range. Coastal Kenya Colony; Tanganyika Territory and "Zanzibar," south to Nyasaland.

Aparallactus capensis capensis Smith Cape Centipede-eater

1849. *Aparallactus capensis* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 16: "Kaffirland eastward to Cape Colony," i.e. Natal, South Africa.

1849. *Elapomorphus capensis* A. Smith, Illus. Zool. S. Africa, Rept. App., p. 16: "Kaffirland eastward of Cape Colony," i.e. Natal, South Africa.

1863. *Cercocalamus collaris* Günther, Ann. Mag. Nat. Hist., (3) **11**, p. 21, pl. iii, fig. A: "Central America" (error).

1895. *Aparallactus punctatolineatus* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 173: Angola.

Range. Tanganyika Territory; Zanzibar and Mafia Islands: south through Mozambique; Nyasaland and the Rhodesias to Cape Province (East London), northwest through Bechuanaland to Angola.

Subfamily DASYPELTINAE

Genus **DASYPELTIS** Wagler[151]

[150] *A. guentheri* was based on the ring-necked young, *uluguruensis* on the uniformly plumbeous adult.

[151] Statements to the contrary notwithstanding, the gender of *Dasypeltis* is feminine. At the time this check list goes to press the genus is undergoing revisionary study by Carl Gans.

1829. *Anodon* A. Smith (not of Oken:1815),[152] Zool. Journ., **4**, p. 443. Type by monotypy: *A. typus* Smith = *Coluber scaber* Linnaeus.

1830. *Dasypeltis* Wagler, Nat. Syst. Amphib., p. 178. Type by monotypy: *Coluber scaber* Linnaeus.

1830. *Analcis* Wagler, Nat. Syst. Amphib., p. 191, footnote 3. New name for *Anodon* A. Smith (preoccupied).

1833. *Rachiodon* Jourdan, Le Temps (Paris:13.vi.1833), p. ?. New name for *Anodon* A. Smith (preoccupied).

1834. *Raphiodon* Jourdan (misprint) L'Institut (de la France: Paris) **2**, p. 214, corrected to *Rachiodon* on p. 223.

1845. *Deirodon* Owen, Odontography; or, A Treatise on the Comparative Anatomy of the Teeth . . . (London), p. 220. New name for *Anodon* A. Smith (preoccupied).

1846. *Dirodon* Agassiz, Nomen. Zool., Index Univers., p. 127. Emendation for *Deirodon* Owen.

Dasypeltis scabra (Linnaeus)[153] Common Egg-eater

1758. *Coluber scaber* Linnaeus, Syst. Nat., ed. 10, 1, p. 223: "in Indis," i.e. South Africa.[154]

1829. *Anodon typus* A. Smith, Zool. Journ., **4**, p. 443: Near Capetown, Cape Province, South Africa.

1853. *Rachiodon abyssinus* A. M. C. Duméril (*nomen nudum*), Mem. Acad. Sci. (Paris), **23**, p. 71: A casual reference to Cartin (misspelled Quartin) Dillon's specimen from Ethiopia.

1854. *Rachiodon Abyssinus* Duméril & Bibron, Erpét. Gén., **7**, p. 496: "Abyssinia," i.e. Ethiopia.

1864. *Dasypeltis scaber* var. *capensis* Peters, Monatsb. Akad. Wiss. Berlin, p. 644, footnote: Cape of Good Hope, i.e. South Africa.

1864. *Dasypeltis scaber* var. *mossambicus* Peters, Monatsb. Akad. Wiss. Berlin, p. 644, footnote: Boror and Tete, Mozambique.

1864. *Dasypeltis scaber* var. *breviceps* Peters, Monatsb. Akad. Wiss. Berlin, p. 645, footnote: "Kaffirland," i.e. South Africa.

1878. *Dasypeltis lineolatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 206: Kitui, Ukamba, Kenya Colony.

1912. *Dasypeltis scabra* var. *atra* Sternfeld, Wiss. Ergebn, Deutsch. Zentral-Afrika-Exped. 1907-1908, **4**, p. 272: Virgin forest behind boundary mountains on northwest shore of Lake Tanganyika, Belgian Congo.

1954. *Dasypeltis scabra loveridgei* Mertens, Zool. Anz., **152**, p. 213:

[152] Suppressed in favor of *Dasypeltis* in 1956 (cf. Opin. Declar. Inter. Comm. Zool. Nomencl., **12**, p. 241. Opinion 387).

[153] Dr. Gans points out that the species *scabra*, which may possibly be subject to some racial subdivision, includes the specimens that in 1942 I referred to "*s. scaber*" and "*s. palmarum*." It is on Dr. Gans' advice that *medici* and *fasciata* are now treated as full species.

[154] Cf. Flower, 1933, Proc. Zool. Soc. London, p. 818.

Finkenstein Farm near Windhoek, Southwest Africa.

Range. Southern Arabia and Somalia, south to Natal, west to the Cape, northwest to the Gold Coast, east through the southern Sudan to Ethiopia.

Dasypeltis medici lamuensis Gans

1957. *Dasypeltis medici lamuensis* Gans, Breviora (Cambridge, Mass.), No. 79, p. 1: Lamu Island, Kenya Colony.

Range. Reddish laterite or gray alluvial soils of coastal Somalia, south through Kenya Colony to the vicinity of Kilimanjaro on the frontier of Tanganyika Territory.

Dasypeltis medici medici (Bianconi)

1859. *Dipsas Medici* Bianconi, Mem. Accad. Sci. Bologna, **10**, p. 501, pl. xxvi (reprinted as p. 277 of Spec. Mossamb.): Mozambique.

1868. *Dasypeltis scaber* var. *fasciolata* Peters, Monatsb. Akad. Wiss. Berlin, p. 451; Zanzibar Island.

1888. *Dasypeltis elongata* Mocquard, Mem. Cent. Soc. Philom. Paris, p. 131, pl. xii, fig. 2: Zanzibar Island.

1893. *Dasypeltis scabra* var. *bianconii* "Med." Boettger (*lapsus* for var. *medici* Bianconi), Zool. Anz., **16**, p. 133.

Range. Reddish laterite soils of the Kenya Colony — Tanganyika Territory frontier (as far inland as Kilimanjaro); Zanzibar and Mafia Islands; south to Mozambique and Nyasaland.

Dasypeltis fasciata (Smith) Western-Forest Egg-Eater

1844. *Dipsas carinatus* Hallowell (not of Schlegel:1837), Proc. Acad. Nat. Sci. Philadelphia, p. 119: "Africa," later (1857, *loc. cit.*, p. 69) amended to Liberia.

1849. *Dasypeltis fasciata* A. Smith, Illus. Zool. S. Africa, Rept., foot note to pl. lxxiii: Sierra Leone.

1859. *Rachiodon subfasciatus* A. Duméril (*nomen nudum*), Arch. Mus. Hist. Nat. (Paris), **10**, p. 198: casual mention of name.

1863. *Rachiodon scaber* var. *subfasciatus* Jan (*nomen nudum*), Elenco Sist. Degli Ofidi, p. 106: Gold Coast.

1863. *Rachiodon scaber* var. *unicolor* Jan (part: *nomen nudum*), Elenco Sist. Degli Ofidi, p. 106: Gold Coast.

1907. *Dasypeltis macrops* Boulenger, Ann. Mag. Nat. Hist., (7) **19**, p. 324: Efulen, French Cameroon.

Range. Western Uganda, west through the Belgian Congo and Cameroons to Gambia.

Family ELAPIDAE

Genus **ELAPSOIDEA** Bocage

1866. *Elapsoidea* Bocage, Jorn. Sci. Lisboa, **1**, pp. 50, 70. Type by monotypy: *E. güntherii* Bocage.

1896. *Elapechis* Boulenger, Cat. Snakes Brit. Mus., **3**, p. 358, footnote. Substitute name for *Elapsoidea* Bocage.

Elapsoidea sundevallii güntherii Bocage Western Garter-Snake

1866. *Elapsoidea Güntherii* Bocage, Jorn. Sci. Lisboa, **1**, pp. 50 ,70, pl. i, figs. 3-3b: Bissau, Portuguese Guinea and Cabinda, Portuguese Congo.

1897. *Elapechis moebiusi* Werner, Verh. Zool. Bot. Ges. Wien, **47**, p. 400: Kete, Gold Coast.

Range. Northern and Western Tanganyika Territory, through western Kenya Colony and Uganda, west to Senegal.

Elapsoidea sundevallii loveridgei Parker
Northeastern Garter-Snake

1949. *Elapsoidea sundevallii loveridgei* Parker, Zool. Verhand. Rijksmus. Nat. Hist. Leiden, No. 6, p. 95: Machakos, Kenya Colony.

Range. Central and eastern Kenya Colony.

Elapsoidea sundevallii nigra Günther Eastern Garter-Snake

1888. *Elapsoidea nigra* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 322: "Ushambola, Zanzibar," i.e. Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of the Usambara; Magrotto and Uluguru Montains, eastern Tanganyika Territory.

Elapsoidea sundevallii decosteri Boulenger
Southeastern Garter-Snake

1888. *Elapsoidea Decosteri* Boulenger, Ann. Mag. Nat. Hist., (6) **2**, p. 141: Delagoa Bay, Mozambique.

1895. *Elapsoidea Boulengeri* Boettger, Zool. Anz., **18**, p. 62: Boroma, Zambezi, Mozambique.

Range. Southern Province of Tanganyika Territory, south through Mozambique, Nyasaland and the Rhodesias to the Transvaal.

Genus **BOULENGERINA** Dollo[155]

1886. *Boulengerina* Dollo, Bull. Mus. Roy. Hist. Nat. Belgique, **4**, p.

[155] For Bogert's reasons for synonymizing *Limnonaja*, see Bogert, 1943, Bull. Amer. Mus. Nat. Hist., **81**, pp. 296, 300.

159. Type by monotypy: *B. stormsi* Dollo.

1923. *Limnonaja* Schmidt, Bull. Amer. Mus. Nat. Hist., **49**, p. 124. Type by monotypy: *Boulengerina christyi* Boulenger.

Boulengerina annulata stormsi Dollo Tanganyika Water-Cobra

1886. *Boulengerina stormsi* Dollo, Bull. Mus. Roy. Hist. Nat. Belgique, **4**, p. 160, fig. —: Lake Tanganyika, Belgian Congo.

Range. Lake Tanganyika and its shores off Tanganyika Territory and Belgian Congo.[156]

Genus **NAJA** Laurenti

1768. *Naja* Laurenti, Syn. Rept., p. 90. Type by tautonomy: *Coluber naja* Linnaeus.[157]

1820. *Naia* Merrem, Vers. Syst. Amphib., pp. 15 (bis), 147, 190. Emendation for *Naja* Laurenti (*Naja* on p. 15 (primus)).

1830. *Uraeus* Wagler, Nat. Syst. Amphib., p. 173. Type by monotypy: *Coluber haje* Linnaeus.

1830. *Aspis* Wagler (not Laurenti:1768), Nat. Syst. Amphib., p. 173. Type by monotypy: *Coluber naja* Linnaeus.

1831. *Tomyris* Eichwald, Zool. Spec. Rossiae Poloninae, Part 3, p. 171. Type by monotypy: *T. oxiana* Eichwald = *Coluber naja* Linnaeus.

Naja haje haje (Linnaeus) Egyptian Cobra

1758. *Coluber haje* Linnaeus, Syst. Nat., ed. 10, **1**, p. 225: Lower Egypt.

1768. *Cerastes candidus* Laurenti, Syn. Rept., p. 83: Libya.

1789. *Coluber Candidissimus* Lacépède, Hist. Nat. Quad. Ovip. Serpens, **2**, Table Methodique, p. 86, text p. 118: Libya.

1854. *Naja Intermixta* Duméril & Bibron, Erpét. Gén., **7**, p. 1299: Based on pl. xix of A. Smith, 1849, so South Africa.

1854. *Naja haje* var. *annulifera* Peters, Monatsb. Akad. Wiss. Berlin, p. 624: Tete, Mozambique.

1873. *Naja haje* var. *viridis* Peters, Monatsb. Akad. Wiss. Berlin, p. 411, pl. i, fig. 1: West Africa.

[156] The locality data for the two British Museum specimens allegedly from Nyasaland had best be regarded with suspicion pending confirmation. Mr. J. C. Battersby informs me (16.i.57) that they were collected by Surgeon H. M. Hanschell, R.N., for the London School of Tropical Medicine which, in 1926, turned them over to the British Museum.

[157] Stejneger (1936, Copeia, p. 140) states that Laurenti's six included species are all synonyms of *Coluber naja* Linnaeus. Prior action by Boie (1826, Isis von Oken, col. 981) in designating *Vipera haemachatea* Latreille as type of *Naja* is inadmissable.

Included in the synonymy by some authors is *Lepidon* Swainson (1839, **2**, p. 345). However, no type was designated, the name simply appearing in a key between *Naia* and *Elaps* with the scant description: Head broad, neck not expansive. *If* East African this might apply to *Pseudohaje* or *Elapsoidea*.

Range. Spanish Morocco east to Egypt, south through Uganda, Kenya Colony, Tanganyika Territory and Zanzibar Island. In fact almost all Africa except for the area of *N. h. barotseensis* Angel (with 15 midbody scale-rows) known only from Lealui, Northern Rhodesia; and the area occupied by *N. h. anchietae* Bocage (with 17 midbody scale-rows) which ranges through the Rhodesias, Bechuanaland, Southwest Africa and Angola. Another race occurs in Arabia.

Naja nigricollis pallida Boulenger Pink-or-red Spitting-Cobra

1896. *Naia nigricollis* var. *pallida* Boulenger, Cat. Snakes Brit. Mus., **3**, p. 379: Inland from Berbera, British Somaliland (restricted by Bogert:1942), also Lake Rudolf.

Range. On red murram soils from northern Ghana and Sudan east to British Somaliland, south through Kenya Colony (Voi to Kibwezi) to Tanganyika Territory (vicinity of Longido Mountain).

Naja nigricollis nigricollis Reinhardt Common Spitting-Cobra

1843. *Naja nigricollis* Reinhardt, Danks. Vidensk. Selsk. Skrift., **10**, p. 369, pl. iii, figs. 5 and 7: Guinea.

1854. *Naja mossambica* Peters, Monatsb. Akad. Wiss. Berlin, p. 625: Sena and Tete, Mossambique.

1893. *Naja nigricollis* var. *crawshayi* Günther, Proc. Zool. Soc. London, p. 620: Lake Mweru, Northern Rhodesia.

1895. *Naja nigricollis* var. *occidentalis* Bocage, Herp. Angola Congo, p. 135; Dondo; Huilla; Humbe; Quisange; and Quilengues, Angola.

1895. *Naja nigricollis* var. *melanoleuca* Bocage (not of Hallowell:1857), Herp. Angola Congo, p. 136: Caconda and Catumbella, Angola.

1955. *Naja nigricollis atriceps* Laurent, Revue Zool. Bot. Afr., **51**, p. 135: Mugera, 1450 metres, Ruyigi Territory, Urundi, Belgian Ruanda-Urundi.[158]

Range. Savanna areas of almost all Africa south of 25° N. (except where occupied by recognizable races), thus including Uganda; Kenya Colony; Tanganyika Territory; Pemba and Zanzibar Islands.

[158] Specimens from Mangasini and other localities in Tanganyika Territory are listed among the paratypes. Like most cobras *nigricollis* is very variable as regards color, and several striking variants may occur in a single locality. Many races not listed here have been described. An overall study of the genus is much to be desired.

Naja melanoleuca Hallowell Black-and-White Cobra[159]

1857. *Naia haie* var. *melanoleuca* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 61: Gabon, French Congo.

1885. *Naja haje* var. *leucosticta* Fischer, Jahrb. Hamburg. Wiss. Anst., **2**, p. 115, pl. iv, fig. 11: Cameroon and Ogooué River, French Congo.

1955. ?*Naja melanoleuca subfulva* Laurent, Revue Zool. Bot. Afr., **51**, p. 132: Lwiro, 1850 metres, Kabare Territory, Kivu, Belgian Congo.

Range. Forested areas of much of Africa south of 15° N. in the West, to the Equator in the East, including Uganda, Kenya Colony, Tanganyika Territory and Zanzibar Island.

Genus **PSEUDOHAJE** Günther

1858. *Pseudohaje* Günther, Cat. Snakes Brit. Mus., p. 222. Type by monotypy: *P. nigra* Günther.

Pseudohaje goldii (Boulenger) Black Forest-Cobra

1895. *Naia goldii* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 34: near Asaba, Nigeria.

1896. *Naia yakoma* Mocquard, C.-R. III Congres Internat. Zool., Leyde, 1895, p. 233: Yakoma, Abiras District, northern Belgian Congo.

Range. Forested areas of Uganda, southwest to Southwest Africa, northwest to Nigeria.

Genus **DENDROASPIS** Schlegel

1848.[160] *Dendroaspis* Schlegel, Versl. Zool. Gen. Amsterdam, p. 5. Type by monotypy: *Elaps jamesoni* Traill.

1852. *Dinophis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 203. Type by monotypy: *D. hammondii* Hallowell = *Leptophis viridis* Hallowell.

1855. *Dendroechis* Fischer, Programm Realschule, Johann. Hamburg, pp. 20, 68. Type by monotypy: *D. reticulata* Fischer = *Leptophis viridis* Hallowell.

1856. *Dendraspis* A. Duméril (not of Fitzinger:1843), Revue Mag. Zool., (2) **8**, p. 558. Emendation for *Dendroaspis* Schlegel.

[159] The few specimens I have taken in the southeast (Mikindani, T. T.; Nyasaland) were a variegated brown, not black as at Kaimosi, K. C. Whether the brown cobras really occupy a well-defined range so that Laurent's name might be applied to them, is not clear. Material in the Museum of Comparative Zoology suggests there is no such division in scale-counts between southeast and west as is shown by Laurent's data.

[160] Date uncertain, but communicated by Schlegel to a meeting held on March 13, 1848 (*fide* Brongersma, 1936, Zool. Meded., **19**, p. 136).

Dendroaspis jamesoni kaimosae Loveridge
Eastern Jameson's Mamba

1936. *Dendraspis jamesoni kaimosae* Loveridge, Proc. Biol. Soc. Washington, **49**, p. 64: Kaimosi, Kakamega, Kenya Colony.

Range. Western Kenya Colony, west through Uganda to Belgian Ruanda-Urundi and the eastern Belgian Congo.

Dendroaspis angusticeps (Smith) Common Green Mamba

1849. *Naia angusticeps* A. Smith, Illus. Zool. S. Africa, Rept., pl. lxx: Natal, South Africa.

1865. *Dendraspis intermedius* Günther, Ann. Mag. Nat. Hist., (3) **15**, p. 97: Zambezi River, Mozambique.

1907. *Dendraspis sjöstedti* Lönnberg, in Sjöstedt, Wiss. Ergeb. Schwed. Zool. Exped. Kilimandjaro, Meru umgeb Massaisteppen, No. **4**, p. 17, pl. i, fig. 2: "Kibonoto," i.e. Kibongoto, Mount Kilimanjaro, Tanganyika Territory.

Range. Kenya Colony; Tanganyika Territory and Zanzibar Island, south through Mozambique, Nyasaland and the Rhodesias to Natal.[161]

Dendroaspis polylepis antinorii Peters[162]
Northern Brown-Mamba

1873. *Dendraspis antinorii* Peters, Monatsb. Akad. Wiss. Berlin, p. 411, pl. i, fig. 2: "Ansaba," i.e. Anseba, Eritrea.

Range. Eritrea, south through Ethiopia and British Somaliland to Mount Moroto, northeastern Uganda, and Murri, northern Kenya Colony.

Dendroaspis polylepis polylepis Günther
Southern Brown-Mamba

1864. *Dendraspis polylepis* Günther, Proc. Zool. Soc. London, p. 310: Zambezi River, Mozambique.

1907. *Dendraspis mamba* Gough, Zool. Anz., **32**, p. 454: White River Settlement, near Nelspruit, Lydenburg District, Transvaal.

Range. Southern Kenya Colony and Tanganyika Territory, south through Mozambique; Nyasaland and the Rhodesias to Natal, west to Southwest Africa, northeast through Angola to the eastern Belgian Congo.

[161] This is the correct distribution, confused for a century by the inclusion of records pertaining to *D. p. polylepis*, etc.

[162] For discussion on the validity of this race, see Parker (1949, Zool. Verh. Rijksmus. Nat. Hist. Leiden, No. 6, p. 98). This, and typical *polylepis* are the snakes commonly called "Black Mambas," though they are not black; the young are grey green, somewhat darker than the vivid fresh green of young *and* adult *angusticeps*.

Family HYDROPHIIDAE

Genus **PELAMIS** Daudin

1803. *Pelamis* Daudin (part), Hist. Nat. Rept., **7**, p. 361. Type by designation of Fitzinger:1843: *P. bicolor* Daudin = *Anguis platura* Linnaeus.[163]

1816. *Pelamys* Oken, Lehrb. Naturg., **3**, Part 2, pp. vi, xv, 279. New name for *Pelamis* Daudin (part) with type by monotypy: *Anguis platuro* (*sic*) Linnaeus.

1817. *Ophinectes* Rafinesque, Amer. Monthly Mag., **1**, p. 432. Type by present designation: *O. luteus* Rafinesque.[164]

1848. *Elaphrodytes* Gistel, Naturg. Thierr., p. ix. New name for *Hydrus* Schneider (*fide* Stejneger:1907. Not seen.).

1910. *Pelamydrus* Stejneger, Proc. U. S. Nat. Mus., **38**, p. 111. Type by monotypy: *Anguis platura* Linnaeus.

Pelamis platurus (Linnaeus) Parti-colored Sea-Snake

1766. *Anguis platura* Linnaeus, Syst. Nat., ed. 12, **1**, p. 351: No locality.

1799. *Hydrus Bicolor* Schneider, Hist. Amphib., **1**, p. 242 (based on Seba, 1735, Thesaurus **2**, pl. lxxvii, fig. 2): Mexico?

1817. *Pelamis schneideri* Rafinesque (new name for *Hydrus bicolor* Schneider, var.), Amer. Monthly Mag., **1**, p. 432.

1817. *Ophinectes luteus* Rafinesque, Amer. Monthly Mag., **1**, p. 433: No locality.[165]

1837. *Hydrophis pelamis* Schlegel (new name for *Anguis platura* Linnaeus), Essai Phys. Serp., **1**, p. 508.

1842. *Pelamis ornata* Gray, Zool. Misc., p. 60: Borneo.

1854. *Pelamis bicolor* var. *variegata* Duméril & Bibron, Erpét. Gén., **7**, p. 1337: Celebes.

1854. *Pelamis bicolor* var. *sinuata* Duméril & Bibron, Erpét. Gén., **7**, p. 1338: No locality.

1856. *Hydrophis* (*Pelamis*) *bicolor* var. *alternans* Fischer (new name for *variegata* Duméril & Bibron), Abhand. Nat. Ver. Hamburg, **3**, p. 63.

1872. *Hydrophis bicolor* var. *maculata* Jan, Icon. Gén. Ophid., livr. 40, pl. iii: Indian Ocean.

[163] For lengthy discussion on rejection of *Hydrus* Schneider by Malcolm Smith (1926, Monogr. Sea-Snakes, p. 116), see H. M. Smith and E. H. Taylor (1945, U. S. Nat. Mus. Bull. **187**, p. 176, footnote).

[164] Rafinesque states that his new genus differs from *Pelamis* in its "carinated or angular abdomen," and the species *lutcus* is characterized as "entirely yellow." It, and doubtless some or all of the other "species" of *Ophinectes* he describes, is apparently but a variant of the highly variable *Anguis platura* Linnaeus.

[165] As pointed out in the preceding footnote to the genus *Ophinectes*, possibly several other "species" attributed to this genus are also synonyms that should be added to the above list.

1921. *Hydrus platurus* var. *subobscurus* Wall, Snakes of Ceylon, p. 422 (name for var. C of Boulenger:1896): Ceylon.

1921. *Hydrus platurus* var. *pallidus* Wall, Snakes of Ceylon, p. 422 (name for var. D of Boulenger:1896): Travancore, India.

1955. *Pelamis platura* vars. *brunnea; fasciata; leucostriata; neurileucura; neuricatenata; tricolor* Deraniyagala, Colored Atlas of some Vertebrates of Ceylon (Colombo), **3**, p. 80; no precise localities mentioned, merely "Ceylon waters."

Range. Indian and other tropical oceans as far as the coast of Mexico in the Pacific Ocean. Occasionally temperate seas such as those of South Africa and around New Zealand in the southern hemisphere; as far north as the Russian Coast Province in the northern hemisphere.[166]

Family VIPERIDAE

Genus **ATRACTASPIS** Smith

1849. *Atractaspis* A. Smith, Illus. Zool. S. Africa, Rept., footnote to text of pl. lxxi. Type by monotypy: *A. bibronii* Smith.

1854. *Brachycranion* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 99. Type by monotypy: *B. corpulentum* Hallowell.

1862. *Eurystephus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 337. Type by monotypy: *Elaps irregularis* Reinhardt.

1895. *Clothelaps* Cope, Trans. Amer. Philos. Soc., **18**, p. 211. Type by present designation: *Atractaspis congica* Peters.

1906. *Melanelaps* Wall, Journ. Bombay Nat. Hist. Soc., **17**, p. 27. Type by monotypy: *M. mcphersoni* Wall = *Atractaspis andersonii* Boulenger.

Atractaspis microlepidota microlepidota Günther[167]

Small-scaled Burrowing-Adder

[166] I am unaware of any actual specimens of *platurus* from Kenya Colony, Tanganyika Territory or Zanzibar Island; reported "sea-snakes" invariably proved to be highly colored muraenid eels. However, *P. platurus* has been taken along the Red Sea coast of Somalia; in the Seychelles and Madagascar, while "It is known from all parts of the coast of East Africa, where it is not uncommon south of the equator," according to Malcolm Smith (1943, Fauna British India, **3**, Serpentes, p. 477).

[167] Laurent, in his revision of the genus *Atractaspis* (1950:10) regards *fallax* as an eastern race of *microlepidota*, whose typical form he restricts to the southern Sudan, but I am far from happy regarding the numerous races of *microlepidota* postulated by Laurent. In the first place the type locality of *fallax* is *not* in Tanganyika Territory as assumed by Laurent, but "drei Tagereisen von Kiriama" and that is clearly shown on the map of Von der Decken's itinerary (1869, Reisen in Ost-Africa, *1*, part *1*, map iii; also cf. part *2*, 1871, pp. 64, 435) as about halfway between Bura and Mombasa. In later years (1897) Tornier corrupted the spelling to "Kircamo."

When adequate series are available it is interesting to note the extensive range of variation of typical *microlepidota*. For example 14 ♂♂ from Torit, Sudan, have a ventral range of 216-239; subcaudals 25-29; 9 ♀♀, also from Torit, have 233-242 ventrals; 21-24 subcaudals. The sexes and extremes have been carefully checked in these snakes (M.C.Z. 53535-53557).

1866. *Atractaspis microlepidota* Günther, Ann. Mag. Nat. Hist., (3) **18**, p. 29, pl. vii, fig. 3: "Probably West Africa" (error).

1866. *Atractaspis fallax* Peters, Monatsb. Akad. Wiss. Berlin, p. 890: "Kiriame" corrected to "Kiriama" = Giriama, Kenya Colony.

1913. *Atractaspis phillipsi* Barbour, Proc. Biol. Soc. Washington, **26**, p. 148: Singa, Sennar Province, Sudan.

Range. Southern Sudan, east through Ethiopia to Somalia, south to Kenya Colony.[168]

Atractaspis irregularis bipostocularis Boulenger[169]

Eastern Variable Burrowing-Adder

1905. *Atractaspis bipostocularis* Boulenger, Ann. Mag. Nat. Hist., (7) **15**, p. 190: Fort Hall near Mount Kenya, Kenya Colony.

1908. *Atractaspis conradsi* Sternfeld, Sitzb. Ges. Naturf. Freunde Berlin, p. 94: Ukerewe Island, Lake Victoria, Tanganyika Territory.

1930. *Atractaspis schoutedeni* Witte, Revue Zool. Bot. Afr., **19**, p. 224, figs. 1-3: "N'Goma," i.e. Goma, Lake Kivu, Belgian Congo.

1934. *Atractaspis babaulti* Angel, Bull. Soc. Zool. France, **59**, p. 169: Kadjudju, Kivu region, Belgian Congo.

1945. *Atractaspis irregularis loveridgei* Laurent, Revue Zool. Bot. Afr., **38**, p. 322: Bunia, Ituri region, Belgian Congo.

Range. Kenya Colony and northwest Tanganyika Territory, west through Uganda and Belgian Ruanda-Urundi to the eastern Belgian Congo.

Atractaspis aterrima Günther

Western-Forest Burrowing-Adder

1863. *Atractaspis aterrima* Günther, Ann. Mag. Nat. Hist., (3) **12**, p. 363: West Africa.

[168] Unknown from Uganda, for Lodwar, though west of Lake Rudolf is in Kenya Colony (not Uganda as stated by Parker:1949:109); the unique ♀ with 37 midbody scale-rows and 245 ventrals, allegedly from "Lake Tanganyika" according to Sir John Kirk who sent it to the British Museum, is scarcely assignable to this form.

[169] Proceeding from east to west across Africa there is a gradual, but definite, increase in scale-rows from 21 (Fort Hall) to 25-27 (*i. irregularis* at Ganta, Liberia). *A. bipostocularis* was founded on a juvenile with two postoculars (no second specimen has been taken in fifty years). I regard this condition as aberrant, for in our series of 23 *m. microlepidota* from Torit, Sudan, two ♀♀ (M.C.Z. 53554-5) have two postoculars on the right side of the head but the normal single scale on the left. If this view is accepted, then the name *bipostocularis* should take precedence over *conradsi* (which was also founded on an aberrant individual as I demonstrated by collecting normal *"irregularis"* on Ukerewe Island. Apart from Laurent's Eritrean *i. angeli*, and his *i. uelensis* from the Congo, which are both apparently recognizable by high ventral counts, the question arises as to how many forms one should recognize — 21-23, 23-25, 25-27, or just two, viz. 21-23 with some overlap of 25 in Uganda and eastern Congo, and 25-27 for the western *i. irregularis* (inc. *parkeri* Laurent, if the subcaudal counts are not found to overlap with more material).

Range. Virgin forest of Uluguru Mountains, Tanganyika Territory, northwest to Uganda, west to Portuguese Guinea.

Atractaspis bibronii rostrata Günther[170]

Zanzibar Bibron's Burrowing-Adder

1868. *Atractaspis rostrata* Günther, Ann. Mag. Nat. Hist., (4) **1**, p. 429, pl. xix, fig. 1: Zanzibar.

1901. *Atractaspis katangae* Boulenger, Ann. Mus. Congo, (1) **2**, p. 13, pl. v, fig. 2: Lofoi, Katanga, Belgian Congo.

1901. *Atractaspis coarti* Boulenger, Ann. Mus. Congo, (1) **2**, p. 14, pl. v, fig. 3: Albertville, Belgian Congo.

Range. Kenya Colony and Tanganyika Territory (Zanzibar coast; possibly Zanzibar Island), south to Mozambique (north of the Zambezi), west through Nyasaland and Northern Rhodesia to southern Belgian Congo.

Genus **CAUSUS** Wagler

1830. *Causus* Wagler, Nat. Syst. Amphib., p. 172. Type by monotypy (as *Naja V-nigrum* Boie is a synonym): *Sepedon rhombeata* Lichtenstein.

1842. *Distichurus* Hallowell, Journ. Acad. Nat. Sci. Philadelphia, **8**, p. 337. Type by monotypy: *D. maculatus* Hallowell = *Sepedon rhombeata* Lichtenstein.

1862. *Heterophis* Peters, Monatsb. Akad. Wiss. Berlin, p. 276. Type by monotypy: *H. resimus* Peters.

1882. *Dinodipsas* Peters, Sitzb. Akad. Wiss. Berlin, p. 893. Type by monotypy: *D. angulifera* Peters = *Aspidelaps lichtensteinii* Jan.

Causus rhombeatus (Lichtenstein)[171] Rhombic Night-Adder

1823. *Sepedon rhombeata* Lichtenstein, Verz. Doubl. Mus. Zool. Berlin, p. 106: No locality.

1827. *Naja Col(uber) v nigrum* Cuv. (*sic*) Boie, Isis von Oken, **20**, col. 557: Africa.

1842. *Distichurus Maculatus* Hallowell, Journ. Acad. Nat. Sci. Philadelphia, **8**, p. 337, pl. xix: Liberia.

[170] To this form all East African records of *bibronii* (to which can be added Tornier's misidentifications of *"irregularis"* from Tanga, etc.) are referable. Laurent has shown that *rostrata* is distinguishable by normally having 23 mid-body scale-rows (rarely 21 or 22), whereas *b. bibronii* A. Smith — with a range south of the Zambezi to Angola — has 21 scale-rows (rarely 23).

[171] I am not prepared to say that this common reptile, which (except for Eritrea, Southwest Africa, and the offshore islands) has been reported from every political unit in Africa south of 20° N., does not break up into some races. I would point out, however, that small populations of uniformly colored, and presumably striped individuals also, are scattered over much of the range and occur together with normally marked specimens. They do not seem to be any more entitled to racial recognition than *Vipera dorsalis* Gray does in Britain.

1905. *Causus rhombeatus* var. *bilineatus* Boulenger, Ann. Mag. Nat. Hist., (7) **16**, p. 114: Between Benguela and Bihe, Angola.

1912. *Causus rhombeatus* var. *taeniata* Sternfeld, Wiss. Ergebn. Deutsch. Zentral-Afrika-Exped. 1907-1908, **4**, p. 276: No. locality (but Schubotz coll., so probably between Lakes Victoria and Kivu).

1955. *Causus lineatus* Laurent, Revue Zool. Bot. Afr., **51**, p. 136: Seram Research Station, Kundelungu Plateau, Kasenga Territory, Upper Katanga, Belgian Congo.

Range. Sudan east to British Somaliland, south through Uganda, Kenya Colony and Tanganyika Territory to Natal, northwest to Angola and French West Africa (Mauretania and French Soudan).

Causus resimus (Peters) Velvety-green Night-Adder

1862. *Heterophis resimus* Peters, Monatsb. Akad. Wiss. Berlin, p. 277, pl. —, fig. 4: Jebel Ghule, Sennar, Sudan.

1888. *Causus Jacksonii* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 331: Lamu, Kenya Colony; Lake Tanganyika, Tanganyika Territory.

1893. *Causus nasalis* Stejneger, Proc. U. S. Nat. Mus., **16**, p. 735: Tana River, Kenya Colony; Cunga, Angola; also West Africa.

1895. *Causus resimus* var. *angolensis* Bocage, Herp. Angola Congo, p 148: Rio Dande and eight other localities in Angola.

Range. Sudan, east to British Somaliland, south through Uganda; Kenya Colony and Tanganyika Territory to Mozambique, west through Northern Rhodesia to eastern Belgian Congo and Belgian Ruanda-Urundi.

Causus defilippii (Jan) Snouted Night-Adder

1862. *H(eterodon) De Filippii* Jan, Arch. Zool. Anat. Fisiol., **2**, p. 225: Africa.

1863. *Causus* (*Heterophis*) *rostratus* Günther, Ann. Mag. Nat. Hist., (3) **12**, p. 363: Ugogo, Tanganyika Territory.

Range. Coastal Colony; Tanganyika Territory and Zanzibar Island (at Mtende), south through Mozambique; Nyasaland and the Rhodesias to Natal.

Causus lichtensteinii (Jan)

1859. *Aspidelaps Lichtensteinii* Jan, Revue Mag. Zool., p. 511: Gold Coast.

1882. *Dinodipsas angulifera* Peters, Sitzb. Akad. Wiss. Berlin, p. 893, pl. xv: "Laguna, near Puerto Cabello, Venezuela" (error).

Range. Western Kenya Colony and Uganda, west to Spanish Guinea; French and British Cameroons; Nigeria; Liberia.

Genus **VIPERA** Laurenti

1768. *Vipera* Laurenti (part), Syn. Rept., p. 99. Type by designation of Fitzinger:1843: *Vipera redii* Gmelin = *Coluber francisci redi* Laurenti = *Coluber aspis* Linnaeus.

1816. *Berus* Oken, Lehrb. Naturg., **3,** Part 2, p. 234. Type by tautonomy: *Coluber berus* Linnaeus.

1820. *Pelias* Merrem, Vers. Syst. Amphib., p. 148. Type by monotypy: *Coluber berus* Linnaeus.

1822. *Chersea* Fleming, Phil. Zool., **2,** p. 295. Type by monotypy: *"Cerastes vulgaris"* ? = *Vipera vulgaris* Latreille = *Coluber aspis* Linnaeus.

1834. *Rhinaspis* Bonaparte, Icon. Fauna. Ital., Anfibi, part. 42. Type by monotypy: *Coluber ammodytes* Linnaeus.

1842. *Daboia* Gray, Zool. Misc., p. 69. Type by subsequent designation: *Vipera elegans* Daudin = *Coluber russellii* Shaw.

1843. *Rhinechis* Fitzinger, Syst. Rept., p. 28. Type by original designation: *Coluber ammodytes* Linnaeus.

1843. *Chersophis* Fitzinger, Syst. Rept., p. 28. Type by original designation: *Vipera elegans* Daudin = *Coluber russellii* Shaw.

1844. *Echidnoides* Mauduyt, Herpétol Vienne, p. 29. Type by original designation: *E. trilamina* Millet = *Coluber berus* Linnaeus.

1927. *Mesocoronis* Reuss, Zool. Anz., **71,** p. 216. Type by original designation: *M. coronis* Reuss = *Vipera berus* var. *bosniensis* Boettger.

1927. *Teleovipera* Reuss, Zool. Anz., **73,** p. 125. Type by original designation: *Coluber ammodytes* Linnaeus.

1927. *Acridophaga* Reuss, Zool. Anz., **73,** p. 126. Type by original designation: *Pelias ursinii* Bonaparte.

1927. *Mesovipera* Reuss, Zool. Anz., **73,** p. 126. Type by original designation: *Coluber aspis* Linnaeus.

1927. *Macrovipera* Reuss, Zool. Anz., **73,** p. 126. Type by original designation: *Coluber lebetinus* Linnaeus.

1927. *Mesohorinis* Reuss, Naturforscher, **4,** p. 129. Misprint for *Mesocoronis* Reuss.

1929. *Latastea* Reuss, Wochenschr. Terrar. Aquar.-Kunde, **26,** p. 64. Type by original designation: *Vipera latastei* Bosca.

1929. *Tzarevseya* Reuss, Wochenschr. Terrar. Aquar.-Kunde, **26,** p. 64. Type by original designation: *Mesocoronis* (*Tzarevseya*) *tigrina* Reuss = *Vipera kaznakovi* Nikolski.

1935. *Latasteopara* Reuss, Nachr.-Blatt. Aquar.-Terrar.-Ver., p. 216. Type by original designation: *Vipera hugyi* Schinz.

Vipera hindii Boulenger Montane Viper

1910. *Vipera hindii* Boulenger, Ann. Mag. Nat. Hist., (8) **5,** p. 513:

Fort Hall, 4000 feet, Kenya Colony.[172]

Range. Kinangop and Aberdare Mountains, Kenya Colony.

Vipera superciliaris Peters Lowland Viper

1854. *Vipera superciliaris* Peters, Monatsb. Akad. Wiss. Berlin, p. 625: Mainland opposite Querimba Island, Cape Delgado, Mozambique.

Range. Mwaya, Lake Nyasa, Tanganyika Territory and Mozambique.

Genus **BITIS** Gray

1768. *Cobra* Laurenti,[173] Syn. Rept., p. 103. Type by designation of Fitzinger:1843: *Coluber atropos* Linnaeus.

1820. *Echidna* Merrem (part; not Forster:1788), Vers. Syst. Amphib., p. 150. Type by designation of Fitzinger:1843: *E. arietans* Merrem.

1842. *Clotho* Gray (not Faujas de Saint-Fond:1808), Zool. Misc., p. 69. Type by tautonomy: *Cobra clotho* Laurenti.

1842. *Bitis* Gray, Zool. Misc., p. 69. Type by tautonomy: *Coluber bitis* (*sic:* error for *bitin*) Bonnaterre = *Cobra lachesis* Laurenti.

1845. *Calechidna* Tschudi, Fauna Peruana, Herp., p. 60. Type by monotypy: *Echidna ocellata* Tschudi = *Coluber atropos* Linnaeus.

Bitis worthingtoni Parker Kenya Horned Viper

1932. *Bitis worthingtoni* Parker, Journ. Linn. Soc. London, Zool., **38**, p. 221: Lake Naivasha, Kenya Colony.

Range. Uplands of Kenya Colony.

Bitis arietans arietans (Merrem)[174] Puff Adder

1768. *Cobra lachesis* Laurenti, Syn. Rept., p. 104: No locality.

1768. *Cobra clotho* Laurenti, Syn. Rept., p. 104: "Ceylon and Cuba" (error).

1789. *C(oluber) Bitin* Bonnaterre, Tabl. Encycl. Méthod. Règnes Nat., Ophiol., p. 22: "Ceylon" (error).

[172] One wonders whether the type actually came from Fort Hall, or was merely sent by Dr. S. L. Hinde when stationed there.

[173] Suppressed in favor of *Bitis* in 1945 (cf. Opin. Declar. Inter. Comm. Zool. Nomencl., **3**, pp. 77-89: Opinion 188).

[174] Actually the correct name is *lachesis*, which has been used less than a dozen times since it was revived by Stejneger. As it has long been associated generically with the Tropical American pit-vipers, the sooner it is officially suppressed the better. Between 1849 and 1949 *Bitis arietans* has been consistently used over 250 times in the literature. The English name, which has come to stay, is also somewhat unfortunate for, while the burrowing-adders and night-adders are all oviparous, the "puff adder" is a truly viviparous "viper."

1798. *Coluber intumescens* Donndorf, Zool. Beytrage Linn. Natur., **3**, p. 209: (not seen).

1802. *Vipera severa* Sonnini & Latreille (part), Hist. Nat. Rept., **3**, p. 335, pl. —, fig. 1: "Japan" (error).

1820. *Vipera* (*Echidna*) *arietans* Merrem, Vers. Syst. Amphib., p. 152: Cape of Good Hope, i.e. South Africa.

1822. *Vipera inflata* Burchell, Travels S. Africa, **1**, p. 469: "Cape Colony," i.e. Cape Province, South Africa.

1829. *Vipera brachyura* Cuvier, Règne Animal, ed. 2, **2**, p. 90: No locality.

1842. *Clotho lateristriga* Gray, Zool. Misc., p. 69: Gambia.

Range. Africa (outside forested areas) from southern Morocco east to Arabia; south (except for an undefined area centering about British Somaliland where *B. a. somalica* Parker occurs) through Uganda; Kenya Colony; Tanganyika Territory (and possibly Zanzibar on the basis of a single specimen collected by Kirk, though not necessarily on the island) to Natal, west through Cape Province, northwest to Morocco.

Bitis arietans somalica Parker

1949. *Bitis lachesis somalica* Parker, Zool. Verhand. Rijksmus. Nat. Hist. Leiden, No. 6, p. 101: Bohodle, 2100 feet, British Somaliland.

Range. British Somaliland, south to northern Kenya Colony.

Bitis gabonica gabonica (Duméril & Bibron)
Central African Gaboon Viper[175]

1854. *Echidna Gabonica* Duméril & Bibron, Erpét. Gén., **7**, p. 1428, pl. lxxx b: Gabon, French Congo.

Range. Southern Sudan and Uganda; eastern Tanganyika Territory[176] south to Mozambique; west through Northern Rhodesia to Angola; north and West to Togoland where (or in the Gold Coast) it meets with the race *B. g. rhinoceros* Schlegel which ranges westward to French Guinea.

Bitis nasicornis (Shaw) Nose-horned Viper

1802. *Coluber Nasicornis* Shaw, Nat. Miscell., **3**, pl. xciv: Interior of Africa (from the master of a Guinea vessel).

[175] Also known as the River-Jack; the name Rhinoceros Viper, though properly pertaining to the West African race of Gaboon Viper, is best abandoned as it has been so often applied to the Nose-horned Viper.

[176] "Zanzibar" was included by me in 1924 on the basis of Sternfeld's 1910 listing. Doubtless his record, like that of Boulenger in 1896, referred to the opposite coast (now Tanganyika) as it is unknown on the island today. Sternfeld also lists *gabonica* from Damaraland, i.e. Southwest Africa, and Stevenson-Hamilton includes it in the herpetofauna of Kruger Park, Transvaal. Both are omitted from the above range pending confirmation.

1854. *Vipera Hexacera* Duméril & Bibron, Erpét. Gén., **7**, p. 1416, pl. lxxviii b, fig. 2: No locality.

Range. Southern Sudan; western Kenya Colony; Uganda; southwest through Belgian Ruanda-Urundi and the Belgian Congo to Angola; north and west to French Guinea (but unrecorded from Togo and Sierra Leone).

Genus **ECHIS** Merrem

1820. *Echis* Merrem (part), Vers. Syst. Amphib., p. 149. Type by designation of Boie (1826) or Fitzinger (1843): *Pseudoboa carinata* Schneider.

1849. *Toxicoa* Gray, Cat. Snakes Brit. Mus., p. 29. Type by subsequent selection: *Echis arenicola* Boie = *Scythale pyramidum* Geoffroy.

Echis carinatus pyramidum (Geoffroy)

Egyptian Saw-scaled Viper

1827. *Scythale pyramidum* Geoffroy Saint-Hilaire, Rept., in Descr. Egypte, p. 152, pl. vii, fig. 1: Egypt.

1827. *Echis arenicola* Boie, Isis von Oken, **20**, col. 558: North Africa.

1834. *Echis pavo* Reuss, Mus. Senckenberg., **1**, p. 157: Egypt.

1834. *Echis varia* Reuss, Mus. Senckenberg., **1**, p. 160: Ethiopia.

1837. *Vipera echis* Schlegel, Essai Phys. Serp., **2**, p. 583, pl. xxi, figs. 10-11: Africa; Arabia; Bengal, India.

Range. Northern India, west through Persia and Arabia to North Africa, south in arid regions to northern Kenya Colony; Uganda and Gold Coast.[177]

Genus **ATHERIS** Cope

1849. *Chlorocchis* Bonaparte, Proc. Zool. Soc. London, p. 145, footnote. Type by tautonomy: *Vipera chloroechis* Schlegel.[178]

1862. *Atheris* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 337. Type by monotypy: *Vipera chloroechis* Schlegel.

1863. *Poecilostolus* Günther, Ann. Mag. Nat. Hist., (3) **11**, p. 25. Type by monotypy: *P. burtonii* Günther = *Echis squamiger* Hallowell.

[177] Possibly the Gold Coast form is separable. *E. c. carinatus* Schneider occurs in a limited area around Madras, India.

[178] *Chlorocchis* was rejected by Boulenger on the grounds that it was inadequately described. However, Bonaparte refers to the green color of this true, but arboreal, viper from Ashanti, and his evident intention was to erect a genus whose type by tautonomy was *Vipera chloroechis* Schlegel.

Atheris squamiger (Hallowell) Green Bush-Viper[179]

1854. *Echis squamigera* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 193: Near Gabon River, French Congo.

1863. *Poecilostolus Burtonii* Günther, Ann. Mag. Nat. Hist. (3), **11**, p. 25: Cameroon.

1864. *Atheris polylepis* Peters, Monatsb. Akad. Wiss. Berlin, p. 642: Liberia.

1885. *Atheris Lucani* Rochebrune, Bull. Soc. Philom. Paris (7), **9**, p. 89: Landana, Cabinda.

1885. *Atheris proximus* Rochebrune, Bull. Soc. Philom. Paris (7), **9**, p. 90: Bissarie, Casamance River district, Senegal.

1887. *Atheris anisolepis* Mocquard, Bull. Soc. Philom. Paris (7) **11**, p. 89: "Alim Leketi," presumably Alima Leketi River, French Congo.

1887. *Atheris laeviceps* Boettger, Zool. Anz., **10**, p. 651: Povo Netonna, near Banana, Belgian Congo.

1888. *Atheris subocularis* Fischer, Jahrb. Hamburg. Wiss. Anst., **5**, p. 5, pls. i, fig. 1, and ii, fig. 11: Cameroon.

1955. *Atheris hispida* Laurent, Revue Zool. Bot. Afr., **51**, p. 138: Lutungura, Kivu District, Belgian Congo.

Range. Western Kenya Colony and Uganda; west through Belgian and French Congo to Cameroons and Fernando Po; south to Angola.

Atheris nitschei nitschei Tornier Great Lakes Bush-Viper

1902. *Atheris nitschei* Tornier, Zool. Jahrb. Syst., **15**, p. 589, fig. —: Mpororo Swamp, Tanganyika Territory.

1906. *Atheris woosnami* Boulenger, Ann. Mag. Nat. Hist., (7) **18**, p. 37: Mubuku Valley, Ruwenzori Mountains, Uganda.

Range. Uganda; western Tanganyika Territory; Belgian Ruanda-Urundi; Belgian Congo.

Atheris nitschei rungweensis Bogert
Rungwe Mountain Bush-Viper

1940. *Atheris nitschei rungweensis* Bogert, Bull. Amer. Mus. Nat. Hist., **77**, p. 104, fig. 18: Rungwe Mountain, Tanganyika Territory.

Range. Southwest Tanganyika Territory; Misuku Mountains, northwest Nyasaland and Northern Rhodesia.

[179] Though commonly referred to as "tree-vipers," so far as my experience goes these snakes are usually found in bushes or shrubbery at the forest-edge. Possibly trionomials should be applied to this form if it can be demonstrated that *chlorocchis* (Schlegel) is but a western race ranging from the Gold Coast to Liberia.

Atheris ceratophorus Werner Usambara Mountain Bush-Viper

1895. *Atheris ceratophorus* Werner, Verh. Zool. Bot. Ges. Wien, **45**, p. 194, pl. v, fig. 1: Usambara Mountains, Tanganyika Territory.

Range. Usambara Mountains, Tanganyika Territory.[180]

Atheris barbouri Loveridge Uzungwe Mountain Bush-Viper

1930. *Atheris barbouri* Loveridge, Proc. New England Zool. Club, **11**, p. 107: Dabaga, Uzungwe Mountains, Tanganyika Territory.

Range. Uzungwe and Ukinga Mountains, Tanganyika Territory.

Class AMPHIBIA

Order GYMNOPHIONA[181]

Family CAECILIIDAE[182]

Genus **SCHISTOMETOPUM** Parker

1941. *Schistometopum* Parker, Ann. Mag. Nat. Hist., (11) **7**, p. 17, fig. 4. Type by original designation: *Dermophis gregorii* Boulenger.

Schistometopum gregorii (Boulenger)[183]
Mud-dwelling Caecilian

1894. *Dermophis gregorii* Boulenger, Proc. Zool. Soc. London, p. 646, pl. xl, fig. 4: Ngatana, Tana River, Kenya Colony.

1912. *Boulengerula denhardti* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 199: Tana Region, Kenya Colony.

1913. *Bdellophis unicolor* Boettger, in Voeltzkow, Reise in Ostafrika, **3**, p. 353, pl. xxiii, fig. 18: Lake Peccatoni, near Witu, Kenya Colony.

Range. Coastal Kenya Colony, south to Wami River near Bagamoyo, and Rufigi River near Kilindi, Tanganyika Territory.

Genus **BOULENGERULA** Tornier

1896. *Boulengerula* Tornier, Die Kriechthiere Deutsch-Ost-Afrikas, p. 164. Type by monotypy: *B. boulengeri* Tornier.

[180] The Togo and Gold Coast records are rejected pending definite capture.

[181] APODA of Boulenger, 1882, Cat. Batr. Gradientia s. Caudata and Batrachia Apoda in the Coll. Brit. Mus., p. 88.

[182] *Hypogeophis guentheri* Boulenger, 1882, described as from "Zanzibar," has been shown by Parker, 1941, to be a synonym of *H. rostrata* (Cuvier) of the Seychelles. It is consequently omitted from this list.

[183] The reasons for amalgamating these three "species," following the collection of topotypes of all three, will be found in Loveridge, 1936, Bull. Mus. Comp. Zool., **79**, pp. 375-378.

Boulengerula taitanus Loveridge Taita Mountains Caecilian

1935. *Boulengerula taitanus* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 16: Mount Mbololo at 4800 feet, Taita Mountains, Kenya Colony.

Range. Taita Mountains, Kenya Colony.

Boulengerula changamwensis Loveridge
Changamwe Lowland Caecilian

1932. *Boulengerula changamwensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 381: Changamwe at 192 feet, near Mombasa, Kenya Colony

Range. Kenya Colony (known only from the type locality).

Boulengerula boulengeri Tornier
Usambara Bluish-Gray Caecilian

1896. *Boulengerula boulengeri* Tornier, Die Kriechthiere Deutsch-Ost-Afrikas, p. 164: Usambara Mountains, Tanganyika Territory.

Range. Usambara and Magrotto Mountains, Tanganyika Territory.

Boulengerula uluguruensis Barbour & Loveridge
Uluguru Pink Caecilian

1928. *Boulengerula uluguruensis* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 183: Vituri, 2000 feet, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains, Tanganyika Territory.

Genus **SCOLECOMORPHUS** Boulenger

1883. *Scolecomorphus* Boulenger, Ann. Mag. Nat. Hist., (5) **11**, p. 48. Type by monotypy: *S. kirkii* Boulenger.

1895. *Bdellophis* Boulenger, Proc. Zool. Soc. London, p. 412. Type by monotypy: *B. vittatus* Boulenger.

Scolecomorphus vittatus (Boulenger)

1895. *Bdellophis vittatus* Boulenger, Proc. Zool. Soc. London, p. 412, pl. xxiv, fig. 4: Usambara Mountains, Tanganyika Territory.

Range. Usambara; Magrotto and Uluguru Mountains, Tanganyika Territory.

Scolecomorphus attenuatus Barbour & Loveridge

1928. *Scolecomorphus attenuatus* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 181: Nyingwa, 7500 feet, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains, Tanganyika Territory.

Scolecomorphus kirkii uluguruensis Barbour & Loveridge

1928. *Scolecomorphus uluguruensis* Barbour & Loveridge, Mem. Mus. Comp Zool., **50**, p. 180: Nyingwa, 7500 feet, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains, Tanganyika Territory.

Scolecomorphus kirkii kirkii Boulenger

1883. *Scolecomorphus Kirkii* Boulenger, Ann. Mag. Nat. Hist., (5) **11**, p. 48: "Lake Tanganyika?"

Range. Highlands of southwestern Tanganyika Territory;[184] Nyasaland and Northern Rhodesia (Nyamkolo: *fide* Pitman).

Order SALIENTIA

Suborder OPISTHOCOELA

Family PIPIDAE[185]

Genus **XENOPUS** Wagler

1827. *Xenopus* Wagler, Isis von Oken, **20**, col. 726. Type by monotypy: *X. boiei* Wagler = *Bufo laevis* Daudin.

1829. *Dactylethra* Cuvier, Règne Animal, ed. 2, **2**, p. 107. Type by monotypy: "crapaud lisse de Daudin" = *Bufo laevis* Daudin.

1864. *Silurana* Gray, Ann. Mag. Nat. Hist., (3) **14**, p. 315. Type by monotypy: *S. tropicalis* Gray.

Xenopus clivii Peracca Eritrean Smooth Clawed-Frog

1898. *Xenopus Clivii* Peracca, Boll. Mus. Zool. Anat. Comp. Univ. Torino, **13**, No. 321, p. 3: Adi Caie and Saganeiti, Eritrea.

Range. Eritrea, south through Ethiopia to Lake Rudolf, Kenya Colony.

Xenopus laevis borealis Parker Kenya Smooth Clawed-Frog

1936. *Xenopus laevis borealis* Parker, Ann. Mag. Nat. Hist., (10) **18**, p. 596: Mount Marsabit, Kenya Colony.

Range. Kenya Colony.

Xenopus laevis victorianus Ahl

Tanganyika Smooth Clawed-Frog

[184] I regard Nieden's record of *Bdellophis vittatus* from Ubena as a misidentified *kirkii* for I personally collected this species on the Mufindi-Njombe road, in addition to a large series from Nyasaland.

[185] Formerly referred to the suborder AGLOSSA, the African tongueless frogs are separated by some authors as XENOPIDAE. Besides PIPIDAE the OPISTHOCOELA includes only the DISCOGLOSSIDAE.

1924. *Xenopus victorianus* Ahl, Zool. Anz., **60**, p. 370: Busisi, Smith Sound, Lake Victoria, Tanganyika Territory.

Range. Uganda; Kenya Colony and western Tanganyika Territory, west to Belgian Congo.

Xenopus laevis bunyoniensis Loveridge

Ruanda Smooth Clawed-Frog

1932. *Xenopus laevis bunyoniensis* Loveridge, Proc. Biol. Soc. Washington, **45**, p. 114: Bufundi, Lake Bunyoni, Uganda.

Range. Highland lakes of southwest Uganda; Belgian Ruanda-Urundi and Belgian Congo.

Xenopus laevis petersii Bocage

Angola Smooth Clawed-Frog

1895. *Xenopus Petersii* Bocage, Herp. Angola Congo, p. 187: Ambaca; Benguela; Caconda; Catumbela; Chimboto; Dondo; Huila; Quibula; Quindumbo and Sao Salvador, Angola.

1927. *Xenopus poweri* Hewitt, Rec. Albany Mus., **3**, p. 413, pl. xxiv, fig. 3: Victoria Falls, Zambezi, Northern Rhodesia.

Range. Southwestern Tanganyika Territory, southwest through Northern Rhodesia to Angola.

Xenopus muelleri (Peters) Müller's Smooth Clawed-Frog

1844. *Dactylethra Muelleri* Peters, Ber. Akad. Wiss. Berlin, p. 37: Mozambique (restricted to Tete, Zambezi, by Loveridge).

Range. Southern Sudan (at Gondokoro); Uganda; Kenya Colony; Tanganyika Territory; Zanzibar and Mafia Islands; Mozambique south to Transvaal (*fide* Mertens); west through Nyasaland and Northern Rhodesia to Angola; north and west in arid areas to Dahomey (*fide* Chabanaud).

Suborder PROCOELA

Family BUFONIDAE

Genus **BUFO** Laurenti[186]

1758. *Bufo* A. J. Roesel von Rosenhof, Hist. Nat. Ranarum, p. 69, pl. xxiv. Type by present designation: *B. aquaticus* von Rosenhof

[186] *Bufo* of von Rosenhof appears to have been ignored as pre-Linnaean and not consistently binomial. *Hylaplesia* Schlegel, 1826 (which antedates Bole, 1827) has been relegated to the synonymy of *Dendrobates* by Davis (1935, Zool. Ser. Field Mus. Nat. Hist., **20**, p. 88), whose genus *Cacophryne* (Type: *Hyla borbonica* Tschudi) is a synonym of *Leptophryne* Fitzinger, Syst. Rept. p. 32. Type by original designation: *Bufo cruentatus* Tschudi. *Phryniscus* Wiegmann, 1834, whose type by monotypy is *P. nigricans* Wiegmann = *Atelopus stelzneri* Weyenberg, is also one of the ATELOPODIDAE. *Scutiger* Theobald, 1868, was removed from the synonymy by Boulenger.

equals and antedates *B. calamita* Laurenti.

1768. *Bufo* Laurenti (part), Syn. Rept., p. 25. Type by tautonomy: *B. vulgaris* Laurenti = *Rana bufo* Linnaeus.

1824. *Oxyrhynchus* Spix, Anim. Spec. Testud. Rana. Brasiliam, p. 49. Type by monotypy: *O. naricus* Spix = *Rana typhonia* Linnaeus.

1828. *Chaunus* Wagler, Isis von Oken, **21**, col. 744. Type by monotypy: *C. marmoratus* Wagler (inc. *C. globulosus* Wagler) both = *Bufo granulosus* Spix.

1838. *Osilophus* "Cuv." Tschudi, Class. Batr. Rept., p. 89. Type by monotypy: "*Osilophus typhonius* Cuv." = *Rana typhonia* Linnaeus.

1843. *Phrynoidis* Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo asper* "Kuhl," i.e. Gravenhorst.

1843. *Phrynomorphus* Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo leschenaultii* Duméril & Bibron = *Bufo guttatus* Schneider.

1843. *Docidophryne* Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo agua* Daudin = *Rana marina* Linnaeus.

1843. *Peltophryne* Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo peltocephalus* Duméril & Bibron, i.e. Tschudi.

1843. *Otolophus* "Cuv." Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo margaritifer* Daudin = *Rana typhonia* Linnaeus.

1843. *Eurhina* Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo proboscideus* Wagler = *Rana typhonia* Linnaeus.

1843. *Chilophryne* Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo d'orbignyi* Duméril & Bibron.

1843. *Phryne* Fitzinger, Syst. Rept., p. 32. Type by original designation: *Bufo vulgaris* Laurenti = *Rana bufo* Linnaeus.

1845. *Anaxyrus* Tschudi, Fauna Peruana, Herp., p. 78. Type by monotypy: *A. melancholicus* Tschudi = *Bufo compactilis* Wiegmann.

1849. *Schismaderma* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 28. Type by original designation: *S. lateralis* Smith = *Bufo carens* Smith.

1860. *Adenomus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 371. Type by monotypy: *A. badioflavus* Cope = *Bufo kelaarti* Günther.

1862. *Rhaebo* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 357. Type by monotypy: *Bufo haematiticus* Cope.

1865. *Epidalea* Cope, Nat. Hist. Review, **5**, p. 102. Type by monotypy: *Bufo calamita* Laurenti.

1868. *Otaspis* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 312. Type by monotypy: *Peltaphryne empusa* Cope.

1868. *Pegaeus* Gistel, in Blicke, Leben Natur. Menschen (Leipzig), p.

161. Type by designation of Mertens:1936: *Rana bufo* Linnaeus.

1870. *Nannophryne* Günther, Proc. Zool. Soc. London, p. 401. Type by monotypy: *N. variegata* Günther.

1870. *Ansonia* Stoliczka, Journ. Asiatic Soc. Bengal, **39**, p. 152. Type by monotypy: *A. penangensis* Stoliczka.

1876. *Cranopsis* Cope, Journ. Acad. Nat. Sci. Philadelphia, (N.S.) **8**, p. 96. Type by monotypy: *C. fastidiosus* Cope.

1876. *Crepidius* Cope, Journ. Acad. Nat. Sci. Philadelphia, (N.S.) **8**, p. 97. Type by monotypy: *C. epioticus* Cope.

1876. *Ollotis* Cope, Journ. Acad. Nat. Sci. Philadelphia, (N.S.) **8**, p. 98. Type by monotypy: *O. caerulescens* Cope.

1879. *Dromoplectus* Camerano, Atti. R. Acad. Sci. Torino, **14**, p. 882. Type by monotypy: *Bufo anomalus* Günther = *B. compactilis* Wiegmann.

Bufo carens Smith

1848. *Bufo carens* A. Smith, Illus. Zool. S. Africa, Rept., pl. lxviii, fig. 1: Interior of South Africa.

1849. *Schismaderma lateralis* A. Smith (new name for *Bufo carens* Smith), Illus. Zool. S. Africa, Rept., App., p. 28.

Range. Kenya Colony and Tanganyika Territory, south to Natal, northwest through Bechuanaland to the Belgian Congo.

Bufo brauni Nieden Dead-leaf Toad

1910. *Bufo brauni* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 450: Amani, Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of the Usambara; Magrotto and Uluguru Mountains, Tanganyika Territory.

Bufo regularis regularis Reuss Egyptian Square-marked Toad

1834. *Bufo regularis* Reuss, Mus. Senckenberg., **1**, p. 80: Egypt.

1841. *Bufo pantherinus* Duméril & Bibron (part)[187] Erpét. Gén. **8**, p. 687: Egypt (A. Lefebvre coll.) by present restriction.

1855. *Bufo mosaica* Seetzen, Reise Syria, Paläst., Aegypt. . . ., **3**, p. 492: Egypt.

1858. *Bufo guineensis* Günther (part), Cat. Batr. Sal. Brit. Mus., p. 59: Coast of Guinea (restricted).

1868. *Bufo spinosus* Bocage (not of Daudin:1803), Proc. Zool. Soc. London, 1867, p. 845: Benguela, Angola.

1897. *Bufo garmani* Meek, Field Mus. Nat. Hist. Zool. Series, **1**, p. 176: "Haili," i.e. Halleh, British Somaliland.

[187] Sometimes attributed to Boie, but his *pantherinus*, as well as its use by Tschudi (1838), constitute *nomina nuda*.

1932. *Bufo regularis kisoloensis* Loveridge,[188] Occ. Papers Boston Soc. Nat. Hist., **8**, p. 52: Kisolo, Kigezi district, Uganda.

Range. Except in the northeast (Morocco and Tunisia), present in all African countries from Algeria (Hoggar and Aïr) and Libya (Fezzan) east to Egypt, south through Uganda, Kenya Colony, Tanganyika Territory, Pemba and Zanzibar Islands, to Natal and the Cape, though in some areas as more or less recognizable races, of which many have been described.

Bufo regularis marakwetensis Roux[189]

1935. *Bufo regularis marakwetensis* Roux, Mission Sci. de l'Omo, **3**, Zool., p. 180: Mount Marakwet at 2500 metres, Kenya Colony.

Range. Kenya Colony (known only from the two type ♂ ♂).

Bufo funereus Bocage

1866. *Bufo funereus* Bocage, Jorn. Sci. Lisboa, **1**, p. 77: Duque de Braganca, Angola.

1882. *Bufo benguelensis* Boulenger, Cat. Batr. Sal. Brit. Mus., pp. 299, 475, pl. xix, fig. 3: Benguela, Angola (restricted).

Range. Uganda, southwest to Angola; northwest to Cameroon and Fernando Po (also Dahomey according to Chabanaud:1916).

Bufo camerunensis camerunensis Parker

1936. *Bufo camerunensis camerunensis* Parker, Proc. Zool. Soc. London, p. 153: Oban, Calabar, Nigeria

Range. Uganda, west to Liberia (but as yet unrecorded from Dahomey and Togo).

Bufo latifrons Boulenger Spiny-flanked Toad

1900. *Bufo latifrons* Boulenger, Proc. Zool. Soc. London, p. 435, pl. xxvii, fig. 1: Benito River, Gabon, French Equatorial Africa.

Range. Kenya Colony;[190] French Congo; French and British Cameroons.

[188] Revived by Laurent (1952, Herpetologica, **8**, p. 53) as a full species sympatric with *regularis*. After careful reappraisal of the paratypes, together with the large series that led me to synonymize *kisoloensis*, I find Laurent's allegedly differential characters offer no grounds for recognizing *kisoloensis*.

[189] Without topotypical material it is unwise to suggest that this is a recognizable race, a full species, or perhaps a synonym of *regularis* or some allied species.

[190] The inclusion of this species rests on a toad taken on Mount Kinangop between 2600 and 2700 metres, according to Angel (1925, Rept. et Batr., p. 56, in "Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). Resultats Scientifiques. Vertebrata" (Paris). At my request Mons. Guibé has kindly re-examined this 85 (not 55) mm. specimen, and states (19.i.1957) that in all respects it agrees with the definition of *latifrons* set forth in Parker's (1936, Proc. Zool. Soc. London, p. 153) key, which should be consulted to avoid confusion with *B. c. camerunensis* Parker.

Bufo steindachnerii Pfeffer

1893. *Bufo Steindachnerii* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 103, pl. ii, fig. 8: Kihengo, Tanganyika Territory.

Range. Somalia, south through coastal Kenya Colony to Tanganyika Territory.

Bufo vittatus Boulenger

1906. *Bufo vittatus* Boulenger, Proc. Zool. Soc. London, p. 573, fig. 98: Entebbe, Uganda.

Range. Lower Egypt; Uganda and western Tanganyika Territory.

Bufo parkeri Loveridge

1932. *Bufo parkeri* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 382: Mangasini, Usandawi, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type series).

Bufo urunguensis Loveridge

1932. *Bufo urunguensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 383: Kitungulu, Urungu, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type series).

Bufo ushoranus Loveridge

1932. *Bufo ushoranus* Loveridge, Occ. Papers Boston Soc. Nat. Hist., **8**, p. 45: Ulugu, Ushora, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type series).

Bufo lindneri Mertens

1955. *Bufo lindneri* Mertens, Jahrb. Ver. Vaterl. Naturk. Wurttemberg, **110**, p. 48: Dar es Salaam, Tanganyika Territory.

Range. Tanganyika Territory (known only from the type ♂ and ♀).

Bufo lönnbergi lönnbergi Andersson

1911. *Bufo lönnbergi* Andersson, Svenska Vetensk.-Akad. Handl., **48**, No. 8, p. 35, pl. ii, figs. 4a-b and 6a-b: Mount Kenya, Kenya Colony.

Range. Kenya Colony.

Bufo lönnbergi nairobiensis Loveridge[191]

[191] On geographical grounds this race is very doubtfully distinct, since it has now been taken on Mount Kinangop and the Mau.

1932. *Bufo lönnbergi nairobiensis* Loveridge, Occ. Papers Boston Soc. Nat. Hist., **8**, p. 48: Nairobi, Kenya Colony.

Range. Kenya Colony.

Bufo mocquardi Angel

1924. *Bufo mocquardi* Angel, Bull. Mus. Hist. Nat. Paris, **30**, p. 269: Mount Kenya and Mount Kinangop, Kenya Colony.

Range. Kenya Colony.[192]

Bufo taitanus taitanus Peters[193]

1878. *Bufo taitanus* Peters, Monatsb. Akad. Wiss. Berlin, p. 208, pl. ii, fig. 8: "Taita," i.e. Teita, Kenya Colony.

Range. Kenya Colony; Tanganyika Territory (Iramba Plateau); Mozambique (Chifumbazi).

Bufo taitanus uzunguensis Loveridge

1932. *Bufo taitanus uzunguensis* Loveridge, Occ. Papers Boston Soc. Nat. Hist., **8**, p. 44: Kigogo, Uzungwe Mountains, Tanganyika Territory.

Range. Uzungwe, Ubena and Poroto Mountains, southern Tanganyika Territory.

Bufo micranotis micranotis Loveridge

1925. *Bufo micranotis* Loveridge, Proc. Zool. Soc. London, p. 770, pl. i, fig. 1: Kilosa, Tanganyika Territory.

Range. (Possibly Coastal Kenya Colony on basis of tadpoles from Diani Beach); Tanganyika Territory.

Bufo micranotis rondoensis Loveridge

1942. *Bufo micranotis rondoensis* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 387: Nchingidi, Rondo Plateau, Tanganyika Territory.

Range. (Coastal Kenya Colony if Diani Beach tadpoles are referable to this race); Rondo Plateau, Tanganyika Territory: Jangombe Swamp, Zanzibar (in M.C.Z.).

Bufo anotis Boulenger

1907. *Bufo anotis* Boulenger, Ann. Mag. Nat. Hist., (7) **20**, p. 48, pl. iii: Chirinda Forest, southeast Mashonaland, Southern Rhodesia.

[192] The Angola record of Monard (1937) is certainly erroneous. This little toad is quite distinct from *nairobiensis*.

[193] Many species or races of earless toads have been recorded under this name from neighbouring territories, including Songosongo Island, Tanganyika Territory. All such require careful reappraisal before being included in the range. Other races occur in Nyasaland and Mozambique.

Range. Kilwa, Tanganyika Territory and Southern Rhodesia.[194]

Genus **NECTOPHRYNOIDES** Noble

1926. *Nectophrynoides* Noble, Amer. Mus. Novit., No. 237, p. 15. Type by original designation: *Nectophryne tornieri* Roux.

Nectophrynoides tornieri (Roux) Usambara Viviparous-Toad

1906. *Nectophryne tornieri* Roux, Proc. Zool. Soc. London, **1**, p. 63, pl. ii, fig. 4: Ukami, i.e. Uluguru Mountains, Tanganyika Territory.

1910. *Nectophryne werthi* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 439: Dar es Salaam, Tanganyika Territory.[195]

Range. Usambara; Magrotto and Uluguru Mountains, Tanganyika Territory.

Nectophrynoides vivipara (Tornier) Rungwe Viviparous-Toad

1905. *Pseudophryne vivipara* Tornier, Sitzb. Akad. Wiss. Berlin, **2**, p. 855: Rungwe and Kinga Mountains, Tanganyika Territory (restricted).[195]

Range. Uluguru; Uzungwe; Ukinga; Rungwe and Poroto Mountains, Tanganyika Territory.

Suborder DIPLASIOCOELA

Family RHACOPHORIDAE[196]

Genus **CHIROMANTIS** Peters

1855. *Chiromantis* Peters, Arch. Naturg., **21**, Abt. 1, p. 56. Type by monotypy: *C. xerampelina* Peters.

[194] My early (1925) record of the occurrence of this species in western Tanganyika Territory was based on misidentified *vittatus* (Bukoba) or the subsequently described *ushoranus* (Ushora).

[195] Dar es Salaam is rejected pending confirmation. It may be observed that both *werthi* and some of the cotypes of *vivipara* were allegedly collected in Dar es Salaam by Werth. Werth was a chemist who had a shop in Dar es Salaam. Possibly, like other residents at the coast, he may have spent a vacation at one or other of the mission stations in the nearby Uluguru Mountains where both species occur — and failed to label his specimens. Alternatively some of these arboreal toads may have been brought to Dar es Salaam in clumps of bamboos for planting in the Botanical Gardens. That they would survive is unlikely.

[196] Includes POLYPEDATIDAE. Though included families are predominantly diplasiocoelous, occasional members of the RHACOPHORIDAE and MICROHYLIDAE have procoelous vertebrae. Formerly the four African families of this check list were grouped together as FIRMISTERNIA, but even that arrangement had its arciferal exceptions.

Laurent (1951, Revue Zool. Bot. Afr., **45**, p. 120) suggests a new grouping in which he would remove *Hyperolius* to a new family, the HYPEROLIIDAE, and with it place such ranid genera as *Astylosternus*, *Arthroleptis*, *Hemisus*, etc.

Chiromantis rufescens (Günther)
Western Foam-nest Tree-Frog

1868. *Polypedates rufescens* Günther, Proc. Zool. Soc. London, p. 486: West Africa.

1875. *Chiromantis guineensis* Buchholz & Peters, Monatsb. Akad. Wiss. Berlin, p. 203, pl. i, fig. 1: Victoria, British Cameroon.

Range. Uganda,[197] west through the Belgian Congo to Nigeria.

Chiromantis xerampelina Peters
Southeastern Foam-nest Tree-Frog

1854. *Chiromantis xerampelina* Peters, Monatsb. Akad. Wiss. Berlin, p. 627: Sena and Tete, Mozambique.

1920. *Chiromantis umbelluzianus* Ferreira, Jorn. Sci. Lisboa (2), **8**, p. 205, pls. i-ii: Umbelluzi Bridge, Lourenço Marques district, Mozambique.

Range. Coastal Kenya Colony; Tanganyika Territory and Zanzibar Island, south through Mozambique, Nyasaland and the Rhodesias to Zululand, Natal.

Chiromantis petersii kelleri Boettger
Northern Foam-nest Tree-Frog

1893. *Chiromantis kelleri* Boettger, Zool. Anz., **16**, p. 131: Lake steppe near Laku, and "Abdallah," i.e. Abdulla country north of Webi Valley, Ethiopia.

1900. *Chiromantis kachowskii* Nikolsky, Ann. Mus. Zool. Acad. Sci. St. Pétersbourg, **5**, p. 246: Ferad, Ethiopia.

1916. *Hylambates enantiodactylus* Calabresi, Monit. Zool. Ital. (Firenze), **27**, p. 36, pl. ii, fig. 2: Bardera, Somalia.

1929. *Chiromantis macrops* Ahl, Zool. Anz., **80**, p. 29: Ganda Ali, "Annia" i.e. Ennia Galla, Ethiopia.

Range. Ethiopia and British Somaliland south through Somalia to northern Kenya Colony.

Chiromantis petersii petersii Boulenger
Central Foam-nest Tree-Frog

1882. *Chiromantis petersii* Boulenger, Cat. Batr. Sal. Brit. Mus., p. 93, pl. x, figs. 1-1a: "Interior of East Africa," i.e. Mpwapwa, Ugogo, Tanganyika Territory.

[197] The only Uganda record is that of Loveridge (1942) for a nest taken in Budongo Forest, northwestern Uganda. In 1902 Boulenger listed *xerampelina* from Uganda (apparently without supporting material), but it is far removed from the range of that species.

1929. *Chiromantis albescens* Ahl, Zool. Anz., **80**, p. 30: Pokomoni, (opposite Lamu Island), Kenya Colony.

1929. *Chiromantis fasciatus* Ahl, Zool. Anz., **80**, p. 31: Teita, Kenya Colony; also Ikoma, Tanganyika Territory.

1930. *Chiromantis pygmaeus* Ahl, Zool. Anz., **88**, p. 219: Kibwezi, Kenya Colony.

1931. *Chiromantis pictus* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 213: Kilimatinde, Tanganyika Territory.

1931. *Chiromantis rugosus* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 215: "Langenburg," i.e. Manda, Lake Nyasa, Tanganyika Territory.

Range. Kenya Colony (south of the equator), southwest to central Tanganyika Territory.[198]

Genus **LEPTOPELIS** Günther

1858. *Leptopelis* Günther, Cat. Batr. Sal. Brit. Mus., p. 89. Type by monotypy: *Hyla aubryi* A. Duméril.

1924. *Pseudocassina* Ahl, Mitt. Zool. Mus. Berlin, **11**, p. 8. Type by monotypy: *P. ocellata* Ahl (not *Hylambates ocellatus* Mocquard as it includes *P. rugosa* Ahl (*fide* Ahl).

1941. *Elaphromantis* Laurent, Revue Zool. Bot. Afr., **35**, p. 98. Type by original designations: *Hylambates notatus* Peters.

1941. *Heteropelis* Laurent, Revue Zool. Bot. Afr., **35**, p. 99. Type by original designation: *Leptopelis parkeri* Barbour & Loveridge.

1941. *Taphriomantis* Laurent, Revue Zool. Bot. Afr., **35**, p. 101. Type by original designation: *Cystignathus bocagii* Günther.

1950. *Cryptothylax* Laurent & Combaz, Revue Zool. Bot. Afr., **43**, p. 276. Type by monotypy: *Hylambates greshoffi* Schilthuis.

Leptopelis gramineus (Boulenger)[199]

1898. *Megalixalus gramineus* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova (2) **18**, p. 721, pl. x, fig. 2: Between Badditu and Dime, Somalia.

[198] It might be pointed out that Kenya is included solely on the basis of the types of *albescens, fasciatus* and *pygmaeus*. Much of Ahl's material was subadult and it was on the descriptions that I synonymized them with *petersii* in 1933 (Bull. Mus. Comp. Zool., **74**, p. 390). When the opportunity occurs to examine the Pokomoni type it should be compared with *C. p. kelleri;* also with *xerampelina* which I obtained in series at nearby Witu. The Ikoma *fasciatus* is certainly *p. petersii*, but the Teita specimen was apparently referred to *xerampelina* by an earlier worker. Teita and nearby Kibwezi are faunistically similar, so *pygmaeus* is likely to be specifically identical with the Teita frog.

[199] Admitted to this list on the somewhat slender evidence of four tadpoles from Domorso waterhole near Moyale, recorded by Scortecci in 1940. In the same paper he records four juveniles from Javello Plain near Agheremariani. The only other Ethiopian record is that of Parker (1930) for Wonrambouechi.

Range. Ethiopia and Somalia, south to northern Kenya Colony.

Leptopelis bocagii (Günther)

1864. *Cystignathus bocagii* Günther, Proc. Zool. Soc. London, p. 481, pl. xxxiii, fig. 2: Duque de Braganca, Angola.

1893. *Hylambates angolensis* Bocage, Jorn. Sci. Lisboa, (2) **3**, p. 119: Caconda, Angola.

1893. *Hylambates cynnamomcus* Bocage, Jorn. Sci. Lisboa, (2) **3**, p. 120: Quilengues, Angola.

1904. *Hylambates bocagei* var. *leucopunctata* Ferreira, Jorn. Sci. Lisboa, (2) **7**, p. 113: Gumba, Angola.

1937. *Leptopelis bocagei haasi* Mertens, Abhand. Senckenberg. Naturf. Ges., No. 435, p. 21, fig. 2: Nsombo, Lake Bangweulu, Northern Rhodesia.

Range. Kenya Colony (from Northern Uaso Nyiro), south through Tanganyika Territory to Nyasaland, west through Northern Rhodesia to Southwest Africa, north through Angola to the Belgian Congo.

Leptopelis anchietae (Bocage)

1873. *Hylambates anchietae* Bocage, Jorn. Sci. Lisboa, **4**, p. 226: Mossamedes, Angola.

1895. *Hylambates marginatus* Bocage, Herp. Angola Congo, p. 178: Quisange, Benguela, Angola.

1930. *Hylambates brevipalmatus* Ahl, Zool. Anz., **87**, p. 228: Unyika, Tanganyika Territory.

Range. Southwestern Tanganyika Territory,[200] west to Angola, north through Belgian Congo to the Bamenda District of French Cameroon.

Leptopelis argenteus (Pfeffer)[201]

1893. *Hylambates argenteus* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 100, pl. ii, fig. 3: Marsh south of Bagamoyo, Tanganyika Territory.

Range. Coastal (Bagamoyo to Ruponda) Tanganyika Territory.

[200] Known only from a single record from the southwest (Ahl's type of *brevipalmatus*) for the frogs assigned to *anchietae* by Tornier (1896) were made paratypes of *signifer* by Ahl = *vermiculatus* (Boulenger).

[201] Erroneously referred to the synonymy of *Hylambates maculatus* by me (1930, Proc. Zool. Soc. London, p. 24).

Leptopelis concolor Ahl[202]

1929. *Leptopelis concolor* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 129: "Wito," i.e. Witu, Kenya Colony.

Range. Coastal Kenya Colony, south to Mikindani, Tanganyika Territory.

Leptopelis flavomaculatus (Günther)[203]

1864. *Hyperolius flavomaculatus* Günther, Proc. Zool. Soc. London, p. 310, pl. xxvii, fig. 1: Rovuma Bay, Tanganyika Territory.

1897. *Hylambates johnstoni* Boulenger, Proc. Zool. Soc. London, pp. 801, 803, pl. xlvi, fig. 4: Kondowe to Karonga, Nyasaland (restricted).

Range. Kenya Colony (Ngatana), south through Tanganyika Territory to Mozambique, west through Nyasaland to Southern Rhodesia; also eastern Belgian Congo.

Leptopelis aubryi (Duméril)

1854. *Hyla punctata* Hallowell (not of Schneider:1799), Proc. Acad. Nat. Sci. Philadelphia, p. 193: near Gabon River, French Congo.

1856. *Hyla aubryi* A. Duméril, Revue Mag. Zool., (2) **8**, p. 561: Gabon, French Congo.

1929. *Leptopelis barbouri* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 119: Mount Lutindi, Usambara Mountains, Tanganyika Territory.[204]

Range. Usambara Mountains, Tanganyika Territory; Belgian Ruanda-Urundi, west to Angola, north to Cameroon, west (with gaps) to French Guinea.

Leptopelis notatus christyi (Boulenger)

1906. *Hylambates cubito-albus* Boulenger (part), Ann. Mag. Nat. Hist., (7) **17**, p. 323: only the juvenile cotypes from Lake Albert, Bunyoro, Uganda.[205]

1912. *Hylambates christyi* Boulenger, Ann. Mag. Nat. Hist., (7) **12**, p. 556: Mabira Forest, "Chagwe," i.e. Kyagwe, Uganda.

1929. *Leptopelis budduensis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 119: Northwest Buddu Forest, "Deutsch-Ost-Afrika," i.e. Uganda.

[202] The Mombasa record of *natalensis* (Smith) by Peters (1869) is probably referable to *concolor*, the two species being superficially very alike.

[203] Based on a juvenile, while the synonym was described from an adult; it serves to emphasize the striking age variation presented by members of this genus.

[204] The types (M.C.Z. 13561-71), which neither I nor others who have examined them can distinguish from Cameroon *aubryi* except in size, were never seen by Ahl who had no representatives of the "species."

[205] The name *cubito-albus* should be restricted to the cotypes from Zima, Cameroon.

Range. Virgin forests of Uganda.

Leptopelis vermiculatus (Boulenger)[206]

1909. *Hylambates vermiculatus* Boulenger, Ann. Mag. Nat. Hist., (8) **4**, p. 497: Amani, Usambara Mountains, Tanganyika Territory.

1929. *Leptopelis signifer* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 216: Derema, Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of the Usambara, Magrotto and Rungwe Mountains, Tanganyika Territory.

Leptopelis karissimbensis Ahl

1929. *Leptopelis karissimbensis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 195: Mtulia Gama, Mt. Karisimbi, Belgian Ruanda.

1929. *Leptopelis kivuensis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 206: Kisenyi, Lake Kivu, Belgian Ruanda.

1929. *Leptopelis graueri* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 213: 70 km. west of south end of Lake Edward, Belgian Congo.

1929. *Leptopelis rugegensis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 218: Rugege Forest, Belgian Ruanda.

Range. Virgin forests of southwest Uganda; Belgian Ruanda-Urundi and the Belgian Congo.

Leptopelis parkeri Barbour & Loveridge[207]

1928. *Leptopelis parkeri* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 236, pl. iv, figs. 9-10: Vituri, Uluguru Mountains, Tanganyika Territory.

1929. *Leptopelis martinsseni* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 219: ? Amani or Tanga, Tanganyika Territory.

Range. Virgin forests of Usambara and Uluguru Mountains, Tanganyika Territory.

Leptopelis uluguruensis Barbour & Loveridge

1928. *Leptopelis uluguruensis* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 235, pl. iii, fig. 3: Nyange, Uluguru Mountains, Tanganyika Territory.

1929. *Leptopelis amaniensis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 197: Amani, Usambara Mountains, Tanganyika Territory.

1929. *Leptopelis usambarae* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 205: Usambara Mountains, Tanganyika Territory.

1929. *Leptopelis tanganus* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 221: Tanga, Tanganyika Territory.

[206] The numerous specimens from Usambara localities listed as *rufus* Reichenow by Nieden (1915) are referable to *vermiculatus*.

[207] Some early and one recent record of *rufus* Reichenow are referable to this species.

1929. *Leptopelis grandiceps* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 207: Amani, Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of Usambara and Uluguru Mountains, Tanganyika Territory.

Genus **HYLAMBATES** Duméril

1858. *Hylambates* A. Duméril, Ann. Sci. Nat., (3) **19**, p. 162. Type by monotypy: *H. maculatus* A. Duméril.

1950. *Phlyctimantis* Laurent & Combaz, Revue Zool. Bot. Afr., **43**, p. 274: Type by original designation: *Hylambates leonardi* Boulenger.

Hylambates maculatus Duméril Red-blotched Black Frog

1853. *Hylambates maculatus* A. Duméril, Ann. Sci. Nat., (3) **19**, p. 165, pl. vii, figs. 1-1b and 4: Zanzibar Island.

1944. *Kassina poweri* Hoffman, Soölog. Navors. Nas. Mus. Bloemfontein, **1**, p. 169, figs. 1-3: St. Lucia, Estuary, Zululand.

Range. Kenya Colony; Tanganyika Territory; Zanzibar Island; Mozambique and Nyasaland; Zululand, Natal.

Hylambates verrucosus Boulenger

1912. *Hylambates verrucosus* Boulenger, Ann. Mag. Nat. Hist., (8) **10**, p. 141: Mabira Forest, "Chagwe," i.e. Kyagwe, Uganda.

Range. Uganda and eastern Belgian Congo (*fide* Noble; also Witte).

Genus **KASSINA** Girard[208]

1853. *Kassina* Girard, Proc. Acad. Nat. Sci. Philadelphia, p. 421. Type by monotypy: *Cystignathus senegalensis* Duméril & Bibron.

1864. *Cassina* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 182. Emendation for *Kassina* Girard.

1907. *Paracassina* Perraca, Boll. Mus. Zool. Anat. Comp. Univ. Torino, **22**, No. 553, p. 3. Type by misidentification: *Cystignathus senegalensis* Duméril & Bibron.[209]

1924. ?*Tornierella* Ahl, Mitt. Zool. Mus. Berlin, **11**, p. 10. Type by subsequent designation of Ahl:1926: *T. pulchra* Ahl = ?

[208] This genus, so frequently redescribed on the basis of juveniles or adults in which the vomerine teeth are absent, is much in need of a comprehensive revision.

[209] The description of *Paracassina* was based on two frogs (*senegalensis*) from Toro, Uganda, which Peracca had misidentified as *Cassina obscura* Boulenger. Consequently, as pointed out by Parker (1930, Proc. Zool. Soc. London, p. 31), *Paracassina* cannot be referred to the synonymy of *Mocquardia* Ahl (new name for *Rothschildia* Mocquard, preoccupied by *Rothschildia* Grote:1896).

1937. *Cassiniopsis* Monard, Bull. Soc. Neuchatel. Sci. Nat., **57**, pp. 13, 41. Type by original designation: *C. kuvangensis* Monard.

1939. *Semnodactylus* Hoffman, Soölog. Navors. Nas. Mus. Bloemfontein, **1**, p. 89. Type by monotypy: *S. thabanchuensis* Hoffman.

1940. *Kassinula* Laurent, Revue Zool. Bot. Afr., **33**, p. 313. Type by original designation: *K. wittei* Laurent = *Cystignathus senegalensis* Duméril & Bibron (juv.).

Kassina senegalensis (Duméril & Bibron)[210]

1841. *Cystignathus Senegalensis* Duméril & Bibron, Erpét. Gén., **8**, p. 418: Galam Lakes, Senegal.

1854. *Cystignathus argyreivittis* Peters, Monatsb. Akad. Wiss. Berlin, p. 626: Cabaceira, Mozambique.

1917. *Megalixalus maculosus* Sternfeld, Wiss. Ergebn. Zweiter Deutsch. Zentral-Afrika-Exped. 1910-1911, **1**, p. 501: Duma, Ubangi, French Equatorial Africa.[211]

1930. *Kassina descrticola* Ahl, Zool. Anz., **88**, p. 280: Windhuk, Southwest Africa.

1930. *Kassina modesta* Ahl, Zool. Anz., **88**, p. 281; Marianhill, Natal.

1933. *Cassina angeli* Witte, Revue Zool. Bot. Afr., **23**, p. 172: Lukafu, Kundelungu, Belgian Congo.[212]

1940. *Kassinula wittei* Laurent, Revue Zool. Bot. Afr., **33**, p. 314, figs. 1b and 2 (based on juveniles of from 12.5 to 14 mm.): Kansenia, Belgian Congo.

1942. *Kassina senegalensis ovambocnsis* Hoffman, Soölog. Navors. Nas. Mus. Bloemfontein, **1**, pp. 150, 155, figs. 26-27: Ovamboland, Southwest Africa.

Range. Sudan, east to Ethiopia (and possibly British Somaliland), south through Uganda, Kenya Colony and Tanganyika Territory to Natal, west to Cape Province, north to the Cameroons, west (with some gaps) to Senegal.

Genus **AFRIXALUS** Laurent[213]

[210] Dr. V. FitzSimons informs me (22.x.56) that he regards *Cassina s. intermedia* Werner (1898) as a synonym of *wealii* Boulenger; while *K. poweri* Hoffman (1944) was based on a specimen of *Hylambates maculatus*.

[211] Dr. R. Mertens has found the type of *maculosus* to be a juvenile *senegalensis*.

[212] Dr. R. Laurent recently (1954) revived *angeli* (which I synonymized in 1936) as a subspecies, but on grounds that appear unlikely to stand the test of a thorough, continent-wide study of this group. Such a revisionary examination may well result in additions to the foregoing synonymy.

[213] Originally proposed as a subgenus without designation of type. Whether there is sufficient justification for the separation by Laurent of *Acanthixalus* (for *spinosus* Buchholz & Peters) or *Heterixalus* (for Malagasy members formerly assigned to *Megalixalus*) remains to be seen. *Megalixalus* is certainly monotypic with *seychellensis* as the only species.

1944. *Afrixalus* Laurent, Revue Zool. Bot. Afr., **38**, p. 113. Type by present designation: *Megalixalus fornasinii congicus* Laurent = *Hyperolius dorsalis* Peters.

Afrixalus fornasini fornasini (Bianconi)
Mozambique Banana-Frog

1849.[214] *Euchnemis Fornasini* Bianconi, Nuovi Ann. Sci. Nat., (2) **10**, 1848, p. 107, pl. v, fig. 1; also 1850, Spec. Zool. Mozamb., Rept., p. 23, pl. v, fig. 1: Mozambique.

1854. *Hyperolius bivittatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 627: Boror, Mozambique.

1862. *Hyperolius spinifrons* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 342: Umvoti, Natal.

1913. *Megalixalus fornasinii* var. *unicolor* Boettger, in Voeltzkow, Reise in Ostafrika, **3**, p. 349: Pemba Island, Zanzibar.

1920. *Megalixalus loveridgii* Procter, Proc. Zool. Soc. London, p. 418, fig. 4: Morogoro, Tanganyika Territory.

1930. *Megalixalus dorsimaculatus* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 92: Magrotto, near Tanga, Tanganyika Territory.

Range. Coastal Kenya Colony; Tanganyika Territory; Pemba, Zanzibar and Mafia Islands; Mozambique; Natal and extreme eastern Cape Province (unless *spinifrons* proves to be a recognizable race).

Afrixalus fornasini dorsalis (Peters) Cameroon Banana-Frog

1875. *Hyperolius dorsalis* (Schlegel) Peters, Monatsb. Akad. Wiss. Berlin, p. 206, pl. i, fig. 2: Boutry, Ashanti, Gold Coast, and Victoria, British Cameroon.

1889. *Megalixalus schneideri* Boettger, Ber. Senckenberg. Naturf. Ges., p. 276: Bonamandune (King Bell Dorf), Cameroon.

1941. *Megalixalus fornasinii congicus* Laurent, Revue Zool. Bot. Afr., **35**, p. 120, fig. 1: Buta, Uele, Belgian Congo.

1951. *Afrixalus dorsalis regularis* Laurent, Ann. Soc. Roy. Zool. Belgique, **82**, p. 25, fig. 1: Lambarené, Ogooué River, French Congo.

Range. Uganda, west through Belgian Congo to French Guinea.

Afrixalus fulvovittatus leptosomus (Peters)[215]

[214] April, 1849, according to Sherborn, but Bianconi (1859, Mem. Accad. Sci. Bologna, **10**, p. 498) claims the name (with a single *i* ending) was first published on 4.ii.1847!

[215] In earlier times there was much confusion regarding these frogs; both names were freely applied to specimens from the eastern seaboard which were, in reality, *A. b. brachycnemis* Boulenger. The only places in East Africa where I have encountered *leptosomus* is at Kaimosi, K. C., and Ujiji, T. T. The latter were recorded by me as *brachycnemis*, and I am indebted to Dr. Laurent for examining them and pointing out that they are actually juvenile *leptosomus*.

1877. *Hyperolius leptosomus* Peters, Monatsb. Akad. Wiss. Berlin, p. 619, pl. —, fig. 5: Chinchoxo, Cabinda.

1931. *Hyperolius brevipalmatus* Ahl, Mitt. Zool. Mus. Berlin, **17**, p. 25: Sangmelima, French Cameroon.

1941. *Megalixalus leptosomus upembae* Laurent, Revue Zool. Bot. Afr., **35**, p. 125, fig. 3: Nyonga, Lake Upemba, Belgian Congo.

Range. Sudan; Uganda; western Kenya Colony; western Tanganyika Territory, west to Angola, north to the Cameroons, and possibly Dahomey (*fide* Laurent).[216]

Afrixalus brachycnemis brachycnemis (Boulenger)[217]
Short-limbed Banana-Frog

1896. *Megalixalus brachycnemis* Boulenger, Ann. Mag. Nat. Hist., (6) **17**, p. 403, pl. xvii, fig. 2: Chiradzulu, Nyasaland.

1931. *Hyperolius pygmaeus* Ahl, Mitt. Zool. Mus. Berlin, **17**, p. 22: Tanga, Tanganyika Territory.

1931. *Hyperolius multifasciatus* Ahl, Mitt. Zool. Mus. Berlin, **17**, p. 24: Rungwe, Tanganyika Territory.

1931. *Hyperolius ipianae* Ahl, Mitt. Zool. Mus. Berlin, **17**, p. 43: Ipiana, Tanganyika Territory.

1931. *Hyperolius unicolor* Ahl, Mitt. Zool. Mus. Berlin, **17**, p. 122: Ipiana, Tanganyika Territory.

Range. Eastern Kenya Colony; eastern Tanganyika Territory; Zanzibar and Mafia Islands; Mozambique; Nyasaland.

Afrixalus uluguruensis (Barbour & Loveridge)
Montane Banana-Frog

1928. *Megalixalus uluguruensis* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 231, pl. iii, fig. 2: Vituri, Uluguru Mountains, Tanganyika Territory.

Range. Virgin forests of Usambara; Magrotto and Uluguru Mountains, Tanganyika Territory.

[216] *A. f. fulvovittatus* (Cope), inc. *cittiger* Peters, ranges from northern Nigeria west to Senegal.

[217] Many early East African records of *"fulvovittatus"* and *"leptosomus"* refer to this species. Trinomials are used on account of the western *A. b. wiedholzi* (Mertens:1938), of which *Megalixalus schoutedeni* Laurent is a synonym. As the range of typical *brachycnemis* is largely confined to the coastal region inland to Lake Nyasa, I (1953) was probably wrong in synonymizing the slightly larger *A. b. orophilus* Laurent from the Central African highlands.

Genus **HYPEROLIUS** Rapp[218]

1842. *Hyperolius* Rapp, Arch. Naturg., **8**, Abt. 1, p. 289. Type by monotypy: *H. marmoratus* Rapp.

1864. *Rappia* Günther, Zool. Rec., **1**, p. 130. New name for *Hyperolius* Rapp, thought to be preoccupied by *Uperolia* Gray.

A. Species represented in the Museum of Comparative Zoology by material (often types, paratypes or topotypes) from those countries indicated by an asterisk (*) in **Range.**

Hyperolius viridiflavus viridiflavus (Duméril & Bibron)

1841. *Euonemis viridiflavus* Duméril & Bibron, Erpét. Gén., **8**, p. 528: Ethiopia.

[218] This, to me the most perplexing of all African genera, is still the least understood and most unsatisfactory. In 1931 *Hyperolius* was reviewed by Ernst Ahl, who described 98 additional species, many of which were composites of distinct forms having somewhat similar patterns. Ahl failed to realize that the juvenile livery of many "species" or races is indistinguishable, though differing markedly from that of their respective subadults, which again may be totally unlike the mature frogs. The males of the latter sometimes have *entirely* different markings from those of their own females.

In 1931 Ahl published two voluminous papers, that in Das Tierreich (No. 55, Amphibia Anura, III, xvi + 477 pp.) bears the date "March 1931," and, having figures of the numerous species, is the more useful. The other (Mitt. Zool. Mus. Berlin, **17**, pp. 1-132), presumably intended to appear first for it carries the abbreviation "spec. nov." after each of the new names, is dated "1 April 1931." From it one can obtain type localities and get an idea of what paratypic material (in many instances mistakenly called "cotypen") was at the author's disposal. The seemingly meticulous, and extremely detailed descriptions actually do not cover the variations of Ahl's available material; often they are flagrantly careless and misleading. It is but fair to warn workers that the keys in Das Tierreich are worse than useless, being based on characters of a trivial or variable nature common to a host of forms that differ solely in their striking color patterns. When Ahl's series of "cotypen" was adequate, a selection of them was obtained in 1932 by exchange for the Museum of Comparative Zoology. The availability of this material made it possible for me to synonymize almost 50 of Ahl's alleged species; Laurent has similarly dealt with some others. We have not always agreed; in some instances, no doubt, because of the composite nature of Ahl's "species," its faded condition, or other cogent reasons.

Laurent, who has done more work on this genus than anyone, has himself proposed at least 60 new *Hyperolius*. Following a decade of bewildering nomenclatorial changes in which species were synonymized or revived as racial entities of this or that form, which in turn was liable to be demoted to subspecific rank of something else, Laurent (1951) endeavored to bring order out of chaos by assigning many of these names to subspecific status of much earlier forms like *marmoratus, viridiflavus,* etc. In preparing this check list I hoped to follow Laurent in this laudable effort, but encountered so many geographical difficulties that — in the interests of stability — it seemed advisable to adhere to binomials except where I have previously used trinomials.

Departing from the format used elsewhere in this check list, I have divided these sedge- or tree-frogs into two groups. The first (*A*) contains those species or subspecies represented by material in the Museum of Comparative Zoology (**indicated by an asterisk***) that, as of today, do not seem capable of further synonymization. The **ranges** given have usually been restricted to the country of origin of the type series and its synonyms, together with those countries from which I have, or have seen, material whose identifications I have been able to verify. From what I have said, I hope it will be clear to enthusiastic local amateurs that ranges should not be extended by the inclusion of early extraterritorial records of the same "species," even though identified by a competent herpetologist of the period. Such book work merely perpetuates confusion.

To the second group (*B*, see p. 334) are assigned those "species," usually known only from a single holotype, that I have not seen. In some instances it is possible that the species in question may not even be referable to *Hyperolius*, whose horizontal pupil is the only external character differentiating it from *Afrixalus* — whose pupil is vertical.

Range. Ethiopia, south to Bannissa, Northern Frontier Province, *Kenya Colony.

Hyperolius pachyderma Werner[219]

1908. *Rappia pachyderma* Werner, Sitzb. Akad. Wiss. Wien, 1907, **116**, Abt. 1, p. 1403: Gondokoro, Sudan.

1921. *Rappia burgeoni* Witte, Revue Zool. Afr., **9**, p. 19, pl. v, figs. 2-2b: "Madyu, Uele" = Gangula Madi on Uele River, midway between Bambili and Niangara, Belgian Congo.

1925. *Rappia Rossii* Calabresi, Atti. Soc. Ital. Sci. Nat. (Milano), **64**, p. 121, fig. —: Upper Uele region, Belgian Congo.

1931. *Hyperolius phrynoderma* Ahl, Das Tierreich, no. 55, p. 344, fig. 218: No locality, but collected by Deutsche Zentral-Afrika Expedition.

1931. *Hyperolius oculatus* Ahl, Das Tierreich, no. 55, p. 377, fig. 252: Balaibo, banks of Duki River, Belgian Congo.

Range. *Sudan; *Uganda; *Kenya Colony; *Belgian Congo.

Hyperolius picturatus Peters[220]

1875. *Hyperolius picturatus* "Schlegel" Peters, Monatsb. Akad. Wiss. Berlin, p. 206, pl. ii, fig. 2: Boutry, Ashanti, Gold Coast.

1875. *Hyperolius nitidulus* Peters, Monatsb. Akad. Wiss. Berlin, p. 209, pl. iii, fig. 4: Yoruba, Lagos, Nigeria.

Range. *Western Kenya Colony; *Uganda; *Belgian Congo; *French Congo; Sao Thomé; *French Cameroon; Togoland; Gold Coast; *Ivory Coast! *Liberia; *Sierra Leone.

Hyperolius marginatus Peters

1854. *Hyperolius marginatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 627: Maçanga, Mozambique.

1931. *Hyperolius pictus* Ahl, Das Tierreich, no. 55, p. 301, fig. 176: Crater Lake, Ngosi Volcano, Tanganyika Territory.

1931. *Hyperolius ngoriensis* Ahl, Das Tierreich, no. 55, p. 324, fig. 198: Crater Lake, Ngosi Volcano, Tanganyika Territory.

Range. Montane marshes of southern *Tanganyika Territory; Mozambique and Nyika Plateau, northern *Nyasaland.

Hyperolius goetzei Ahl

1931. *Hyperolius goetzei* Ahl, Das Tierreich, no. 55, p. 413, fig. 286: Uhehe, Tanganyika Territory.

[219] With respect to the first two names (*Rappia pachyderma* was based on a juvenile of generalized appearance), I have followed Laurent (1951) who regards *pachyderma* as a race of *viridiflavus*. Hitherto I have referred to this frog as *rossii*.

[220] The alleged example from Pemba Island, reported by Boettger (1913), on being re-examined by Mertens (1940) was found to be a juvenile *Afrixalus f. fornasini*.

Range. Uplands of *Kenya Colony and *Tanganyika Territory.

Hyperolius discodactylus Ahl

1931. *Hyperolius discodactylus* Ahl, Das Tierreich, no. 55, p. 363, fig. 239: Rugege Forest, Belgian Ruanda-Urundi, and west of Lake Edward, Belgian Congo.

1931. *Hyperolius alticola* Ahl, Das Tierreich, no. 55, p. 379, fig. 255: at 1800 metres, Ruwenzori Mountains, Belgian Congo.

Range. *Ruwenzori Mountains, Uganda; *Belgian Congo.

Hyperolius montanus (Angel)

1924. *Rappia montana* Angel, Bull. Mus. Hist. Nat. (Paris), **30**, p. 269: Mount Kinangop, Aberdare Mountains, Kenya Colony.

Range. Montane marshes of Mts. Kinangop and Kenya, *Kenya Colony.

Hyperolius pantherinus (Steindachner)

1891. *Megalixalus pantherinus* Steindachner, Anz. Akad. Wiss. Wien, **28**, p. 142: Laikipia, Kenya Colony.

Range. Kenya Colony (known only from the holotype: photo in M.C.Z.).

Hyperolius bayoni (Boulenger)[221]

1911. *Rappia bayoni* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (3) **5**, p. 168: Bulolo; Busu; Entebbe; Jinja; Kabulamuliro; and Mbale, Uganda.

1931. *Hyperolius stuhlmanni* Ahl, Das Tierreich, no. 55, p. 395, fig. 271: Vitchumbi, south end of Lake Edward, Belgian Congo.

1940. *Hyperolius ornatus* Laurent, Revue Zool. Bot. Afr., **34**, p. 4: Rutshuru, Belgian Congo.

Range. *Uganda, southwest to Belgian Ruanda-Urundi (also reported from Mozambique by Parker in 1931).

Hyperolius kivuensis Ahl[222]

1931. *Hyperolius kivuensis* Ahl, Das Tierreich, no. 55, p. 280, fig. 151 (34 mm. ♀, Kandt coll.): Lake Kivu, Belgian Congo.

1931. *Hyperolius kwidjwiensis* Ahl, Das Tierreich, no. 55, p. 296, fig. 172 (32 mm. ♂, Schubotz coll.): "Kwidjwi," i.e. Idjwi Island,

[221] A ♀ frog (M.C.Z. 10287) from the Uganda shore of Lake Edward differs slightly from a topotype *stuhlmanni* (M.C.Z. 28126).

[222] In 1951 Laurent regarded *kwidjwiensis* (with which he would include *kandti*) as distinct. He would transfer *koehi* to the synonymy of *schubotzi* Ahl (in whose synonymy I place the 37 mm. *macrodactylus*). The series of frogs from Nyamkolo, Lake Tanganyika, N. Rhodesia which in 1930 I referred to *rhodoscelis* in error, appear to be indistinguishable from Kivu frogs.

Lake Kivu, Belgian Congo.

1931. *Hyperolius kandti* Ahl, Das Tierreich, no. 55, p. 327 (33 mm. ♂, Kandt coll.): Lake Kivu, Belgian Congo.

1931. *Hyperolius koehli* Ahl, Das Tierreich, no. 55, p. 405 (33 mm. ♂, Koehl coll.): Kisenyi, Lake Kivu, Belgian Ruanda-Urundi.

Range. *Southwest Uganda; *western Tanganyika Territory; *Northern Rhodesia; *eastern Belgian Congo; *Belgian Ruanda-Urundi.

Hyperolius variabilis Ahl[223]

1931. *Hyperolius variabilis* Ahl, Das Tierreich, no. 55, p. 297, fig. 173: restricted to Bukoba, Tanganyika Territory.

1931. *Hyperolius wettsteini* Ahl, Das Tierreich, no. 55, p. 343, fig. 217: Bukoba, Tanganyika Territory.

1931. *Hyperolius mohasicus* Ahl, Das Tierreich, no. 55, p. 360, fig. 236: Lake Mohasi, Belgian Ruanda-Urundi.

1931. *Hyperolius monticola* Ahl, Das Tierreich, no. 55, p. 376, fig. 251: "Niansa," i.e. Nyanza, Belgian Ruanda-Urundi.

1931. *Hyperolius irregularis* Ahl, Das Tierreich, no. 55, p. 396, fig. 272: Lake Mohasi, Belgian Ruanda-Urundi.

Range. Montane meadows of southwest *Uganda; Belgian Ruanda-Urundi and adjacent *Belgian Congo.

Hyperolius latifrons Ahl[224]

1931. *Hyperolius latifrons* Ahl, Das Tierreich, no. 55, p. 335, fig. 208: Bamboo forest at 2400 metres, near Mheabu Gahama village. Mount Karisimbi, Belgian Ruanda-Urundi.

1931. *Hyperolius karissimbiensis* Ahl, Das Tierreich, no. 55, p. 348, fig. 223: Bamboo forest at 2400 metres, near Mheabu Gahama village, Mount Karisimbi, Belgian Ruanda-Urundi.

Range. *Western Tanganyika Territory; Belgian Ruanda-Urundi and *Belgian Congo.

Hyperolius multicolor Ahl[225]

1931. *Hyperolius multicolor* Ahl, Das Tierreich, no. 55, p. 367, fig. 243: Bamboo forest at 2400 metres, near Mheabu Gahama village,

[223] Considered a race of *viridiflavus* by Laurent (1951) who would add *punctatissimus* Ahl and *flavoguttatus* (part) to the above synonymy. While Ahl's material was often composite I scarcely think it warrants such action; however, *wettsteini* and *monticola* are added *fide* Laurent.

[224] Both *latifrons* and *karissimbiensis* were based on juveniles of 21 and 23 mm. respectively. Laurent (1951) regards *karissimbiensis* as a distinct race of *viridiflavus* to which he would add *multicolor* Ahl.

[225] Our cotype and series of *multicolor* from Lake Bunyoni (with whose identification Laurent concurs) do not support its synonymization with *"karissimbiensis."*

Mount Karisimbi, Belgian Ruanda-Urundi.

Range. Montane meadows of southwest *Uganda; *Belgian Ruanda-Urundi and adjacent Belgian Congo.

Hyperolius bitaeniatus Ahl[226]

1931. *Hyperolius bitaeniatus* Ahl, Das Tierreich, no. 55, p. 322, fig. 196: Ukonde-Unyika, Tanganyika Territory.

Range. Southwestern Tanganyika Territory and nearby *Northern Rhodesia.

Hyperolius fuelleborni Ahl[227]

1931. *Hyperolius fuelleborni* Ahl, Das Tierreich, no. 55, p. 349, fig. 224: "Langenburg," i.e. Manda, Lake Nyasa, Tanganyika Territory.

Range. Region around northern end of Lake Nyasa, southwest *Tanganyika Territory.

Hyperolius mariae Barbour & Loveridge[228]

1928. *Hyperolius mariae* Barbour & Loveridge Mem. Mus. Comp. Zool., **50**, p. 217, pl. iii, fig. 1: Derema, Usambara Mountains, Tanganyika Territory.

1931. *Hyperolius melanophthalmus* Ahl, Das Tierreich, no. 55, p. 341, fig. 215: Zanzibar.

1931. *Hyperolius renschi* Ahl, Das Tierreich, no. 55, p. 397: Zanzibar.

Range. Coastal *Tanganyika Territory and *Zanzibar Island.[229]

Hyperolius flavoguttatus Ahl[230]

1931. *Hyperolius flavoguttatus* Ahl, Das Tierreich, no. 55, p. 369, fig. 245: Bukoba, Tanganyika Territory.

Range. *Kenya Colony and *Tanganyika Territory.

[226] At one time (1943) Laurent thought *bitaeniatus* might be a synonym of *rhodoscelis* Boulenger (with which he correctly synonymizes *undulatus* Boulenger). A comparison of our *undulatus* cotype with our cotype of *bitaeniatus* convinces me they are distinct. We have also a good series of quite typical *bitaeniatus* from Abercorn. More recently (1951) Laurent has, mistakenly I think, referred *bitaeniatus* to the synonymy of *H. mariae* Barbour & Loveridge.

[227] Laurent (1951) refers *fuelleborni* to the synonymy of *nyassae* Ahl. We have cotypes of both and I cannot agree; to my thinking *"nyassae"* is a synonym of *rhodoscelis* (Boulenger).

[228] Laurent (1951) adds *noblei* Ahl to the synonymy; I adhere to my (1936) alignment of it with *puncticulatus* (Pfeffer).

[229] My earlier record from Lake Nyasa was based on a misidentified *fuelleborni*.

[230] All that the Museum of Comparative Zoology has is a bleached cotype from Bukoba; a correctly colored topotype from Mount Kenya, and a frog from Mount Mbololo somewhat doubtfully attributable to *flavoguttatus*. These do not suggest that Laurent is correct in synonymizing *flavoguttatus* with *variabilis* Ahl.

Hyperolius udjidjiensis Ahl[231]

1931. *Hyperolius udjidjiensis* Ahl (part), Das Tierreich, no. 55, p. 370, fig. 246: restricted to Ujiji, Tanganyika Territory.

Range. *Tanganyika Territory.

Hyperolius striolatus Peters[232]

1882. *Hyperolius striolatus* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 9: "Taita," i.e. Teita, Kenya Colony.

1902. *Rappia ferniquci* Mocquard, Bull. Mus. Hist. Nat. (Paris), **8**, p. 407: Athi River, Kenya Colony.

1931. *Hyperolius caeruleopunctatus* Ahl, Das Tierreich, no. 55, p. 350, fig. 225: Nairobi and Kibwezi, Kenya Colony.

1931. *Hyperolius pulchromarmoratus* Ahl, Das Tierreich, no. 55, p. 367, fig. 242: "British East Africa" (Hübner of Kibwezi).

1931. *Hyperolius udjidjiensis* Ahl (part), Das Tierreich, no. 55, p. 370, fig. 246 (only the paratypes from Kibwezi, Kenya Colony).

1931. *Hyperolius scheffleri* Ahl, Das Tierreich, no. 55, p. 387: Kibwezi, Kenya Colony.

Range. *Kenya Colony.

Hyperolius rhodoscelis (Boulenger)

1901. *Rappia rhodoscelis* Boulenger, Ann. Mus. Congo, (1) **2**, fasc. 1, p. 3, pl. ii, figs. 1-1a: Pweto, Lake Mweru, Belgian Congo.

1901. *Rappia undulata* Boulenger, Ann. Mus. Congo, (1) **2**, fasc. 1, p. 4, pl. ii, fig. 2: Pweto and Lofoi, Lake Mweru, Belgian Congo.

1902. *Rappia symetrica* Mocquard, Bull. Mus. Hist. Nat. (Paris) **8**, p. 408: Athi River, Kenya Colony.

1920. *Rappia platyrhinus* Procter, Proc. Zool. Soc. London, p. 416, fig. 3: Nairobi, Kenya Colony.

1931. *Hyperolius asper* Ahl, Das Tierreich, no. 55, p. 310: Nairobi, Kenya Colony.

1931. ?*Hyperolius breviceps* Ahl, Das Tierreich, no. 55, p. 316, fig. 190 (at least the paratypes from Eldama Ravine, Kenya Colony, are *rhodoscelis*): "Tschimbo" = Chimbo, Mozambique.

1931. *Hyperolius nyassae* Ahl, Das Tierreich, no. 55, p. 339, fig. 213: "Langenburg," i.e. Manda, Lake Nyasa, Tanganyika Territory.

Range. ? *Southern Sudan; *Kenya Colony; *Tanganyika Territory; ? Mozambique; ? *Angola; southern *Belgian Congo.

[231] From Ujiji we have a topotype series consisting of a ♂ and five ♀♀ that I collected in 1939. I regard them as distinct from *striolatus* with which species Laurent (1951) would synonymize *udjidjiensis* (part). It seems questionable whether Ahl's cotype from Kibwezi is conspecific.

[232] To the synonymy of *striolatus*, Laurent would add *symetrica, platyrhinus, asper* and the Baringo specimen of *breviceps* Ahl. Geographically this seems plausible but is incorrect unless the species is dichromatic.

Hyperolius punctatissimus Ahl[233]

1931. *Hyperolius punctatissimus* Ahl, Das Tierreich, no. 55, p. 299, fig. 174: restricted to Bukoba, Tanganyika Territory.

Range. *Tanganyika Territory.

Hyperolius vermicularis Ahl[234]

1893. *Rappia vermiculata* Pfeffer (not of Peters:1882), Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 98, pl. i, fig. 12: Zanzibar.

1931. *Hyperolius vermicularis* Ahl (new name for *vermiculata* Pfeffer, preoccupied by an Angolan species), Das Tierreich, no. 55, p. 275, fig. 145.

Range. *Kenya Colony; Zanzibar Island.

Hyperolius marmoratus ommatostictus Laurent[235]

1951. *Hyperolius marmoratus ommatostictus* Laurent, Ann. Soc. Roy. Zool. Belgique, **82**, p. 36: "Kibonoto," i.e. Kibongoto, Mount Kilimanjaro, Tanganyika Territory.

Range. *Tanganyika Territory.

Hyperolius argentovittis Ahl[236]

1931. *Hyperolius argentovittis* Ahl, Das Tierreich, no. 55, p. 345, fig. 220: Ujiji, Tanganyika Territory.

1931. *Hyperolius callichromus* Ahl (part), Das Tierreich, no. 55, p. 372, fig. 248: Western banks of "Russisi," i.e. Ruzizi River and northwest shores of Lake Tanganyika, Belgian Congo.

[233] Laurent (1951) would synonymize this also with *variabilis* Ahl, but our solitary specimen from Kabare, Bukoba District, seems to show relationship with *striolatus* rather than with *variabilis*.

[234] Laurent (1951) would add *scriptus* Ahl to the synonymy. However, I failed to meet with *vermicularis* in the vicinity of Tanga (from whence came the holotype of *scriptus*), obtaining our abundant material from seven localities north of Mombasa.

[235] The Museum of Comparatve Zoology topotypes (M.C.Z. 21609-11) were taken at the same time as the type series. Kibongoto is not very high, viz. 1300 metres, roughly 4225 feet.

[236] In their tibial pattern our long series of *argentovittis* topotypes form a link with the speckled tibial pattern exhibited by our *callichromus* cotypes (M.C.Z. 17630-1). In the opposite direction — on the southeast shore of Lake Tanganyika — the even larger series I captured at Nyamkolo are remarkably uniform, displaying a single red-brown streak on the tibia that is only occasionally broken up into two or three elongate blotches. Some of our cotypes of *brieni* Laurent (1943, Ann. Mus. Congo Belge, (1) **4**, fasc. 2, p. 119, fig. 36 *only*), viz ♂ and ♀ (M.C.Z. 26264, 26266) have a dorsal pattern, and differ but slightly in tibial pattern, from *argentovittis*. Yet our other cotypes of *brieni* ♂ and ♀ (M.C.Z. 26263, 26265), also from Nyonga, Upper Luapula, have the vermiculated dorsal patterns so admirably portrayed in Laurent's figure 37. They are unquestionably referable to the same form as the frogs from Kabengere, Belgian Congo, that I have referred to *graueri* Ahl. Either *brieni* is a composite, being part *argentovittis* and part *graueri*, or the species is dichromatic, in which case Laurent is correct in adding *graueri* to the synonymy of *argentovittis* and *brieni* should go too. Our cotype (M.C.Z 17633) of *decipiens* Ahl from the Ruzizi lends no support to Laurent's synonymizing of that species with *argentovittis*.

Range. *Tanganyika Territory; *Northern Rhodesia: *Belgian Congo.

Hyperolius puncticulatus substriatus Ahl

Northern Broad-striped Sedge-Frog

1931. *Hyperolius substriatus* Ahl, Das Tierreich, no. 55, p. 358, fig. 234: Magrotto Mountain, Tanganyika Territory.

Range. Coastal *Kenya Colony (Malindi), south through the Usambara Mountains to Morogoro, *Tanganyika Territory; *Zanzibar Island.[237]

Hyperolius puncticulatus puncticulatus (Pfeffer)[238]

Southern Broad-striped Sedge-Frog

1893. *Rappia puncticulata* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 31, pl. ii, fig. 2: Zanzibar.

1931. *Hyperolius noblei* Ahl, Das Tierreich, no. 55, p. 400, fig. 275: Kilwa, Tanganyika Territory.

Range. Zanzibar Island; Uluguru and Rungwe Mountains of *Tanganyika Territory; Misuku; Nyika and Mlanje Mountains of *Nyasaland.

Hyperolius argus ahli Loveridge[239]

Northern Argus-spotted Sedge Frog

1936. *Hyperolius ahli* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 402: Lake Peccatoni, northeast of Witu, Kenya Colony.

Range. Coastal *Kenya Colony, south to Lindi, *Tanganyika Territory.

Hyperolius argus argus Peters[240]

Southern Argus-spotted Sedge-Frog

1854. *Hyperolius argus* Peters, Monatsb. Akad. Wiss. Berlin, p. 628 (based on ♀): Boror, Mozambique.

[237] M.C.Z. 17162 from Mwera, Zanzibar Island, is undoubtedly referable to this form. It remains to be seen which race is dominant on the island.

[238] I disagree with Laurent's action in removing *noblei* from the synonymy of *puncticulatus* to that of *mariae* Barbour & Loveridge. Uganda and other records outside the range given here, are considered questionable.

[239] For a coloured plate showing the striking sexual dichromatism of this race, whose ♂ is green flecked with black, see Loveridge (1942, Bull. Mus. Comp. Zool., **91**, pl. iii).

[240] Admission to this list depends on the identification of the juveniles from Mafia Island reported by Parker (1937), and from the ♀ from Zanzibar recorded by Laurent (1943); both are somewhat questionable. My Tanganyika material identified as *argus* by Procter (1920), and consequently some of my own, were actually referable to *p. substriatus* Ahl (1931). See Parker (1931, Proc. Zool. Soc. London, pl. i) for astonishing age and sexual dichromatism in a near topotypic series.

1854. *Hyperolius flavoviridis* Peters, Monatsb. Akad. Wiss. Berlin, p. 628 (based on ♂): Boror, Mozambique.

1854. *Hyperolius Tettensis* Peters, Monatsb. Akad. Wiss. Berlin, p. 628 (based on ♂): Tete, Mozambique.

1893. *Rappia platycephala* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 96, pl. ii, fig. 2 (based on ♂): Quilimane, Mozambique.

Range. *Mozambique; *Nyasaland.

Hyperolius concolor sansibaricus (Pfeffer)
Northeastern Straw-or-Green Sedge-Frog

1893. *Rappia sansibarica* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 97, pl. ii, fig. 4: Zanzibar.

1931. *Hyperolius rubripes* Ahl, Das Tierreich, no. 55, p. 361: Kililana, mainland opposite Lamu Island, Kenya Colony.

Range. *Kenya Colony; *Tanganyika Territory; Zanzibar Island.[241]

Hyperolius concolor tuberilinguis Smith[242]
Southeastern Straw-or-Green Sedge-Frog

1849. *Hyperolius tuberilinguis* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 26: country eastward of Cape Colony, i.e. Natal.

1862. *Hyperolius coccotis* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 342: Umvoti, Natal.

1864. *Hyperolius citrinus* Günther (part), Proc. Zool. Soc. London, p. 311, pl. xxvii, fig. 2: restricted to "Zambezi Expedition."

1867. ?*Hyperolius granulosus* Peters, Monatsb. Akad. Wiss. Berlin, p. 891, footnote: Mozambique.

1947. *Hyperolius kivuensis smaragdinus* Laurent, Ann. Mag. Nat. Hist., (11) **14**, p. 292: Charre, Mozambique.

1947. *Hyperolius sansibaricus loveridgei* Laurent, Ann. Mag. Nat. Hist., (11) **14**, p. 294: Kitaya, Rovuma River, Tanganyika Territory.

Range. Southern *Tanganyika Territory; Mozambique; *Nyasaland; *Natal.

Hyperolius parkeri parkeri Loveridge
Northeastern Brown-or-Green Sedge-Frog

1933. *Hyperolius parkeri* Loveridge, Bull. Mus. Comp. Zool., **74**, p. 410: Bagamoyo, Tanganyika Territory.

[241] The Uganda record of Roux (1910) must be considered doubtful.

[242] The Charre series on which Laurent based his *smaragdinus*, were originally referred by Parker (1931) to *concolor* (Hallowell) of Liberia. With this determination I can find no fault as Liberian and Natal frogs appear indistinguishable though it appears advisable to treat them as distinct until we know more of the intermediate races — of which *kivuensis* may well be one. The 133 frogs from Kitaya, on some of which Laurent based his *loveridgei*, were originally assigned by me to *c. citrinus* Günther.

Range. Coastal *Kenya Colony, south to Dar es Salaam, *Tanganyika Territory.

Hyperolius parkeri rovumae Loveridge[243]
Southeastern Brown-or-Green Sedge-Frog

1942. *Hyperolius parkeri rovumae* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 410, pl. iii, figs. 5-6: Kitaya, Rovuma River, Tanganyika Territory.

Range. Coastal (Kilwa to Kitaya) *Tanganyika Territory.

Hyperolius nasutus Günther
Sharp-and-blunt-snouted Sedge-Frog

1864. *Hyperolius nasutus* Günther, Proc. Zool. Soc. London, p. 482, pl. xxxiii, fig. 3: Duque de Braganca, Angola.

1895. *Rappia punctulata* Bocage, Herp. Angola Congo, p. 168: Banks of the "Quanza" i.e. Cuanza River, Angola.

1901. *Rappia granulata* Boulenger, Ann. Mus. Congo, (1) **2**, fasc. 1, p. 4, pl. ii, fig. 3: Pweto, Lake Mweru, Belgian Congo.

1901. *Rappia oxyrhynchus* Boulenger, Ann. Mus. Congo, (1) **2**, fasc. 1, p. 5, pl. ii, fig. 4: Pweto and Lofoi, Lake Mwenu, Belgian Congo.

1931. ?*Hyperolius petersi* Ahl, Das Tierreich, no. 55, p. 274, fig. 144: Mombasa, Kenya Colony.

1931. *Hyperolius acuticeps* Ahl, Das Tierreich, no. 55, p. 282, fig. 153: Ukonde-Unyika, Tanganyika Territory.

Range. Ethiopia (*fide* Parker); Uganda (*fide* Loveridge); *Kenya Colony; *Tanganyika Territory; *Nyasaland; *Northern Rhodesia; *Southern Rhodesia; *Angola; *Belgian Congo; French Cameroon (*fide* Mertens:1940); Liberia (as *nasutus* subsp. Laurent:1951); French Guinea (as *oxyrhynchus* subsp. Laurent:1951).

Hyperolius pusillus (Cope)[244] Transparent Pigmy Sedge-Frog

1862. *Crumenifera pusilla* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 343: Umvoti, Natal.

1864. *Hyperolius microps* Günther, Proc. Zool. Soc. London, p. 311, pl. xxvii, fig. 3: Rovuma Bay, Tanganyika Territory.

243 The brown ♂ and green ♀ with white side-stripe are shown in color on plate iii, together with the two sexes of the typical form which lacks a light side stripe.

244 The heavily spotted *milnei* from northeast Kenya may appear to differ from *pusillus* of Natal, but so many intermediate conditions occur along the 2000 miles that separate them it seems advisable to ignore subspecies. Many West African frogs have been referred to *pusillus* in error.

1932. *Hyperolius usaramoae* Loveridge, Proc. Biol. Soc. Washington, **45**, p. 63 (based on ♂): Mogogoni Swamp, south of Dar es Salaam, Tanganyika Territory.

1935. *Hyperolius milnei* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 18 (based on ♀): Witu, Coast Province, Kenya Colony.

1935. *Hyperolius translucens* Power, Proc. Zool. Soc. London, p. 339, figs. 6-7, pl. i, figs. 3-4 (based on ♂ and ♀): Port St. Johns, Pondoland, South Africa.

Range. Coastal *Kenya Colony; *Tanganyika Territory; *Nyasaland; *Natal and adjacent *Cape Province.

B. Species usually known only from the original description, frequently based on a single individual. This list is alphabetically arranged.

Hyperolius albifrons Ahl

1931. *Hyperolius albifrons* Ahl, Das Tierreich, no. 55, p. 354, fig. 230: "Africa."

Range. Mafia Island (*fide* Parker:1937).

Hyperolius albofrenatus Ahl

1931. *Hyperolius albofrenatus* Ahl, Das Tierreich, no. 55, p. 315, fig. 189 (coll. Ule or Uhl): "German East Africa."

Range. Tanganyika Territory.

Hyperolius albolabris Ahl

1931. *Hyperolius albolabris* Ahl, Das Tierreich, no. 55, p. 287, fig. 161 (coll. Neumann: 26.ii.1894): Kwa Buoseh or Buoreh, Tanganyika Territory.

Range. Tanganyika Territory.

Hyperolius bergeri Ahl

1931. *Hyperolius bergeri* Ahl, Das Tierreich, no. 55, p. 346, fig. 221: "Guaso" i.e. Uaso Narok, Kenya Colony.

Range. Kenya Colony.

Hyperolius glandicolor Peters

1878. *Hyperolius glandicolor* Peters, Monatsb. Akad. Wiss. Berlin, p. 208, pl. ii, fig. 9: "Taita," i.e. Teita, Kenya Colony.

Range. Kenya Colony.

Hyperolius guttolineatus Ahl

1931. *Hyperolius guttolineatus* Ahl, Das Tierreich, no. 55, p. 321, fig. 195 (coll. Uhl): "German East Africa."

1951. *Hyperolius marmoratus guttatolineatus* Laurent (*lapsus* for *gut-*

tolineatus Ahl, though page and figure numbers are wrong and should be as cited above), Ann. Sci. Roy. Zool. Belgique, **82**, p. 389.

Range. Tanganyika Territory.

Hyperolius marmoratus campylogrammus Laurent[245]

1951. *Hyperolius marmoratus campylogrammus* Laurent, Ann. Soc. Roy. Zool. Belgique, **82**, p. 36: Bura, 1050 metres, Teita, Kenya Colony.

Range. Kenya Colony.

Hyperolius quadratomaculatus Ahl

1931. *Hyperolius quadratomaculatus* Ahl, Das Tierreich, no. 55, p. 412, fig. 285: Mohoro, Tanganyika Territory.

Range. Tanganyika Territory.

Hyperolius scriptus Ahl

1931. *Hyperolius scriptus* Ahl, Das Tierreich, no. 55, p. 287, fig. 160: Tanga, Tanganyika Territory.

Range. Tanganyika Territory.

Hyperolius tornieri Ahl

1931. *Hyperolius tornieri* Ahl, Das Tierreich, no. 55, p. 304, fig. 179: Ukami, i.e. Uluguru Mountains, Tanganyika Territory.

Range. Tanganyika Territory.

Hyperolius viridiflavus pitmani Laurent

1951. *Hyperolius viridiflavus pitmani* Laurent, Ann. Soc. Roy. Zool. Belgique, **82**, p. 394: Lake Bunyoni, southwest Uganda.

Range. Uganda.

Family RANIDAE[246]

Genus **ARTHROLEPTIDES** Nieden

1910. *Arthroleptides* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 445. Type by monotypy: *A. martiensseni* Nieden.

Arthroleptides martiensseni Nieden

Usambara Montane-torrent-Frog

[245] To which Laurent would assign the Mount Mbololo frog that I refer with misgivings to *flavoguttatus* Ahl.

[246] This is employed in its generally accepted sense. Laurent (1951, Revue Zool. Bot. Afr., **45**, p. 120) has proposed radical changes in which he would transfer *Arthroleptis* and *Hemisus* to a new concept, the HYPEROLIIDAE.

1910. *Arthroleptides martiensseni* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 445: Amani, Usambara Mountains, Tanganyika Territory.

Range. Rocky montane streams of Usambara, Magrotto and Uluguru Montains, Tanganyika Territory.

Arthroleptides dutoiti Loveridge Elgon Montane-torrent-Frog

1935. *Arthroleptides dutoiti* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 17: Koitobos River, 7200 feet, Mount Elgon, Kenya Colony.

Range. Rocky montane streams of Mount Elgon, Kenya Colony.

Genus **RANA** Linnaeus

1758. *Rana* Linnaeus, Syst. Nat., ed. 10, **1**, p. 210. Type by designation of Fitzinger in 1843: *R. temporaria* Linnaeus.

1814. *Ranaria* Rafinesque, Specchio Sci. (Palermo), **2**, No. 10, p. 102. Substitute name for *Rana* Linnaeus.

1838. *Hylarana*[247] Tschudi, Class. Batr. Rept. (reprinted 1839), p. 78. Type by monotypy: *Hyla erythraea* Schlegel.

1838. *Strongylopus* Tschudi, Class. Batr. Rept. (reprinted 1839), p. 79. Type by monotypy: *S. fasciatus* Tschudi.

1838. *Pyxicephalus* Tschudi, Class. Batr. Rept. (reprinted 1839), p. 83. Type by designation of Boulenger in 1920: *P. adspersus* Tschudi.

1841. *Limnodytes* Duméril & Bibron, Erpét. Gén., **8**, p. 510. Substitute name for *Hylarana* Tschudi.

1843. *Pelophylax* Fitzinger, Syst. Rept., p. 31. Type by original designation: *Rana esculenta* Linnaeus.

1843. *Limnophilus* Fitzinger (not of Agassiz:1842), Syst. Rept., p. 31. Type by original designation: *Rana mascareniensis* Duméril & Bibron.

1843. *Euphlyctis* Fitzinger, Syst. Rept., p. 31. Type by original designation: *Rana leschenaultii* Duméril & Bibron = *Rana cyanophlyctis* Schneider.

1843. *Phrynoderma* Fitzinger, Syst. Rept., p. 31. Type by original designation: *Rana cutipora* Duméril & Bibron = *Rana hexadactyla* Lesson.

1843. *Hydrophylax* Fitzinger, Syst. Rept., p. 31. Type by original designation: *Rana malabarica* Tschudi.

1843. *Limnonectes* Fitzinger, Syst. Rept., p. 31. Type by original designation: *Rana kuhlii* Duméril & Bibron.

247 Amended to *Hylorana* by various authors.

1858. *Tomopterna* Günther, Cat. Batr. Sal. Brit. Mus., p. 7. Type by designation of Boulenger in 1920: *Pyxicephalus delalandii* Tschudi.

1858. *Sphaerotheca* Günther, Cat. Batr. Sal. Brit. Mus., p. 20. Type by monotypy: *S. strigata* Günther = *Rana breviceps* Schneider.

1859. *Ranula* Peters, Monatsb. Akad. Wiss. Berlin, p. 402. Type by monotypy: *R. gollmerii* Peters = *Rana palmipes* Spix.

1860. *Dicroglossus* Günther, Proc. Zool. Soc. London, p. 158. Type by monotypy: *D. adolfi* Günther.

1863. *Hoplobatrachus* Peters, Monatsb. Akad. Wiss. Berlin, p. 449. Type by monotypy: *H. ceylanicus* Peters.

1865. *Amolops* Cope, Nat. Hist. Review, **5**, p. 117. Type by monotypy: *Polypedates afghanus* Günther.

1867. *Pohlia* Steindachner, Amphibia, in Reise österr. Fregatte Novara, p. 15. Type by monotypy: *Rana palmipes* Spix.

1868. *Trypheropsis* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 117. Type by original designation: *T. chrysoprasinus* Cope.

1868. *Pachybatrachus* Mivart (not of Kefferstein:1868), Proc. Zool. Soc. London, p. 559. Type by monotypy: *P. robustus* Mivart.

1869. *Clinotarsus* Mivart, Proc. Zool. Soc. London, p. 227. New name for *Pachybatrachus* Mivart (preoccupied).

1881. *Maltzania* Boettger, Abhand. Senckenberg. Naturf. Ges., **12**, p. 417. Type by monotypy: *M. bufonia* Boettger.

1891. *Crotaphitis* Schulze, Jahresb. Naturw. Ver. Magdeburg, 1890, p. 176. Type by designation of Stejneger in 1907: *Rana temporaria* Linnaeus.

1891. *Baliopygus* Schulze, Jahresb. Naturw. Ver. Magdeburg, for 1890, p. 177. Type by designation of Stejneger in 1907: *Rana esculenta* Linnaeus.

1893. *Phrynopsis* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 101. Type by monotypy: *P. boulengerii* Pfeffer = juv. *Pyxicephalus edulis* Peters.

1894. *Levirana* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 197. Type by original designation: *L. vibicaria* Cope.

1907. *Hildebrandtia* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 229. Type by monotypy: *Pyxicephalus ornatus* Peters.

1917. *Aubria* Boulenger, C. R. Acad. Sci. (Paris), **165**, p. 988, footnote. Type by monotypy: *Rana subsigillata* A. Duméril.

1920. *Ptychadena* Boulenger, Rec. Indian Mus., **20**, p. 5. Type by original designation: *Rana mascareniensis* Duméril & Bibron.

1924. *Ranosoma* Ahl, Arch. Naturg., **90**, Abt. A, p. 250. Type by monotypy: *R. scherері* Ahl = *Rana occipitalis* Günther.

1927. *Pseudoxenopus* Barbour & Loveridge, Proc. New England Zool.

Club, **10**, p. 14. Type by original designation: *P. alleni* Barbour & Loveridge.[248]

1931. *Abrana* Parker, Proc. Zool. Soc. London, 1930, p. 898. Type by monotypy: *A. cotti* Parker = *Rana floweri* Boulenger.

1931. *Palcorana* Scortecci, Atti. Soc. Ital. Sci. Nat. (Milano), **70**, p. 17. Type by designation of Parker in 1936: *Rana beccarii* Boulenger.

1931. *Gigantorana*[249] Noble, Biology of the Amphibia (New York), p. 159. Type by monotypy: *Rana goliath* Boulenger.

Rana albolabris albolabris Hallowell

Disk-toed White-lipped Frog

1856. *Rana albolabris* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 153.

1903. *Chiromantis lepus* Andersson, Verh. Zool. Bot. Ges. Wien, **53**, p. 142 (53.5 mm. ex.): Cameroon.[250]

Range. Southern *Sudan; Uganda; western Tanganyika Territory (Bukoba); west to Angola (where it meets with the race *a. parkeriana* Mertens), north to Cameroon, west to Portuguese Guinea.[251]

Rana galamensis bravana (Peters)

1882. *Limnodytes bravanus* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 3: "Barawa," i.e. Brava, Somalia.

1929. *Rana magretti* Scortecci, Atti. Soc. Ital. Sci. Nat. (Milano), **68**, p. 182, pl. ix, figs. 1-3: Ghinda, Eritrea.

1929. *Rana fiechteri* Scortecci, Atti. Soc. Ital. Sci. Nat. (Milano), **68**, p. 248, pl. xii, figs. 2-4: Villaggio Duca degli Abruzzi, Somalia.

1931. *Rana somalica* Scortecci, Atti Soc. Ital. Sci. Nat. (Milano), **69**, p. 320: Villaggio Duca degli Abruzzi, Somalia.

Range. Somalia; coastal *Kenya Colony; *Tanganyika Territory; *Pemba Island; *Zanzibar Island; Mozambique; Nyasaland; Northern Rhodesia; eastern *Belgian Congo.

Rana galamensis galamensis Duméril & Bibron

[248] Based on a subadult without vomerine teeth; the frog is now known as *Rana crassipes alleni* Barbour & Loveridge.

[249] Apparently attributed to Nieden in error.

[250] *C. leptus* is unquestionably a synonym as may be seen from the figure subsequently (1905) published by Andersson. Less certain was Noble's action in synonymizing *R. zenkeri* Nieden, 1908, Mitt. Zool. Mus. Berlin, **3**, p. 497 (92 mm. adult and 8 others), from Bipindi, Cameroon, for it appears recognizable. The Museum of Comparative Zoology has both from Metet, Cameroon.

[251] Of this common arboreal frog the Museum has examples from Sudan; Belgian and French Congo; French Cameroon; Nigeria; Ivory Coast; Liberia; Sierra Leone.

1841. *Rana galamensis* Duméril & Bibron, Erpét. Gén., **8**, p. 367: Galam Lakes, Senegal.

1896. *Rana oubanghiensis* Mocquard, C. R. Soc. Philom. Paris, No. 19, p. 234: "Upper Oubanghi," i.e. Oubangui River, French Equatorial Africa.

Range. *Sudan; *Uganda; Belgian Congo; Belgian Ruanda-Urundi; French and British Cameroon; Nigeria; *Gold Coast: French Guinea; Portuguese Guinea; *Gambia; Senegal.

Rana wittei (Angel)

1924. *Phrynobatrachus Wittei* Angel, Bull. Mus. Hist. Nat. (Paris), **30**, p. 130: Molo, Mau Escarpment, Kenya Colony.

1925. *Rana aberdariensis* Angel, Rept. et Batr., in Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). Résultats scientifiques. Vertebrata. (Paris), **2**, p. 42, pl. ii, figs. 1-2: Mount Kinangop, Aberdare Mountains, Kenya Colony.

Range. Montane marshes of Ethiopia (*fide* Angel); *Kenya Colony and eastern *Belgian Congo.

Rana fuscigula chapini Noble

Montane-forest-stream Dusky-throated-Frog

1924. *Rana chapini* Noble, Bull. Amer. Mus. Nat. Hist., **49**, p. 214, fig. 6a: Batama, Stanleyville district, Belgian Congo.

Range. Forest streams of *Ethiopia; *Uganda; *Kenya Colony; *Tanganyika Territory and *Belgian Congo.

Rana fuscigula angolensis Bocage[252]

Savanna-stream Dusky-throated-Frog

1866. *Rana angolensis* Bocage, Jorn. Sci. Lisboa, **1**, p. 73: Duque de Braganca, Angola.

1893. *Rana nyassae* Günther, Proc. Zool. Soc. London, 1892, pp. 555, 558: Shire Highlands, Nyasaland.

1894. *Rana quecketti* Boulenger, Proc. Zool. Soc. London, p. 643,[253] pl. xxxix, fig. 1: Pietermaritzburg, Natal.

1896. *Rana Nutti* Boulenger, Ann. Mag. Nat. Hist., (6) **18**, p. 467: Lake Tanganyika.

Range. *Uganda; *Kenya Colony; *Tanganyika Territory:

[252] Possibly not separable from *f. fuscigula* from which it is distinguished only by its longer hind legs, a character which it shares with *f. chapini*.

[253] Though *quecketti* was synonymized by Boulenger himself with *f. fuscigula*, with which it appears to agree in limb length, Dr. V. F. FitzSimons informs me (22.x.56) that it does not in the least resemble typical *fuscigula* and should, in his opinion, be assigned to the synonymy of *f. angolensis*. He regards *f. fuscigula* as being more or less confined to the Cape; unfortunately short-limbed individuals are present throughout much of the range of *f. angolensis*.

Mozambique; *Nyasaland; Northern and Southern Rhodesia; Bechuanaland; *Transvaal; *Natal; *Orange River; *Cape Province; *Angola; *Belgian Congo; *Belgian Ruanda-Urundi.

Rana fuscigula fuscigula Duméril & Bibron
Short-limbed Dusky-throated-Frog

1841. *Rana fuscigula* Duméril & Bibron, Erpét. Gén., **8**, p. 386: Cape of Good Hope, i.e. South Africa.

Range. Owing to long confusion with *R. f. chapini* and *R. f. angolensis* little reliance can be placed on records in the literature. I have examined the material on which those from Kenya Colony and Tanganyika Territory were based and found them to be *R. f. chapini*. I have collected frogs conforming to *f. fuscigula* at Mushongero, Lake Mutanda, southwest *Uganda (which may be an area of intermediates as *f. angolensis* was also present there); *Nyasaland; *Bechuanaland Protectorate; *Orange River; *Cape Province.

Rana christyi Boulenger

1919. *Rana christyi* Boulenger, Revue Zool. Afr., **7**, p. 5: "Madié," i.e. Medje, Ituri, Belgian Congo.

Range. *Uganda and *Belgian Congo.

Rana oxyrhynchus gribinguiensis Angel
Montane-forest Sharp-nosed-Frog

1922. *Rana (Ptychadena) Gribinguiensis* Angel, Bull. Mus. Hist. Nat. (Paris), **28**, p. 399, fig. —: Fort Crampel, Lake Chad, French Equatorial Africa.

Range. Streams in montane forest, or recently deforested areas, of *Uganda; *Kenya Colony; *Tanganyika Territory; *Nyasaland; *Belgian Congo; French Congo; French Equatorial Africa; *French Cameroon; Nigeria; Ivory Coast; *Liberia.

Rana oxyrhynchus oxyrhynchus A. Smith
Savanna Sharp-nosed-Frog

1849. *Rana oxyrhynchus* "Sundevall" A. Smith, Illus. Zool. S. Africa, Rept., pl. lxxvii, figs. 2 and 2a-2c: Kaffirland and the region of Port Natal, i.e. Durban, Natal.

1868. *Rana anchietae* Bocage, Proc. Zool. Soc. London, 1867, p. 843, fig. 1 (48 mm. ♂): Benguela, Angola.

1897. *Phrynobatrachus hailensis* Meek, Field Mus. Nat. Hist. Zool. Series, 1, p. 175: "Haili," i.e. Halleh, British Somaliland.

1906. *Rana Theileri* Mocquard, Bull. Mus. Hist. Nat. (Paris), **12**, p. 252: Nelspruit, Transvaal.

1923. *Ptychadena aberae* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 97: Abera, near "Jandjan" (? Jiran), southwest Ethiopia.

1933. *Rana oxyrhynchus migiurtina* Scortecci, Atti Soc. Ital. Sci. Nat. (Milano), **72**, pp. 12, 51, pl. i, fig. 3: Uadi Arro, Somalia.

Range. Chiefly in streams of lowland or plateau savanna in the *Sudan, Eritrea, *Ethiopia, French and *British Somaliland, Somalia, *Uganda Protectorate, *Kenya Colony, *Tanganyika Territory, *Pemba, Zanzibar and Mafia Islands, *Mozambique, *Nyasaland, Northern and *Southern Rhodesia, Bechuanaland Protectorate, *Transvaal, *Natal, *Cape Province, Southwest Africa, Cabinda, Angola, Belgian Congo and *Belgian Ruanda-Urundi. Reported from almost every country in Africa south of 15° N., but many western records may have resulted from confusion with the montane forest race listed above or with *R. o. superciliaris* Günther of Sierra Leone.

Rana floweri Boulenger[254]

1917. *Rana floweri* Boulenger, Ann. Mag. Nat. Hist., (8) **20**, p. 417: Rosaires, Blue Nile, Sudan.

1923. *Rana erlangeri* Ahl, Mitt. Zool. Mus. Berlin, **11**, p. 5: Lake Abaya, northeast of Lake Stephanie, Ethiopia.

1925. *Rana barbouri* Loveridge, Proc. Zool. Soc. London, p. 776, pl. i, fig. 2: Nyambita, Mwanza, Tanganyika Territory.

1931. *Abrana cotti* Parker, Proc. Zool. Soc. London, 1930, p. 898, fig. 1: Charre, Mozambique.

Range. *Egypt (Giza: M.C.Z. 3138-40), Sudan, *Kenya Colony, *Tanganyika Territory, *Mozambique. (I regard the French Cameroon record of Monard, 1951, confirmed by Laurent, as somewhat questionable.)

Rana mascareniensis mascareniensis[255] Duméril & Bibron
Common Mascarene-Frog

[254] For long confused with *o. oxyrhynchus*, from which *floweri* may be distinguished by the fine black vermiculations on its buttocks and shorter hindlimb, whose tibio-tarsal articulation, when directed forwards, reaches only to the eye or nostril (in *o. oxyrhynchus* to end of snout, usually far beyond).

[255] Unless a ♀ (M.C.Z. 28622) from Liwale, southeastern Tanganyika Territory is correctly assigned, so far as I am aware the perfectly valid species or subspecies *R. mascareniensis mossambica* Peters (1854), together with its synonyms *trinodis* var. *Böttgeri* Pfeffer (1893) and *vernayi* FitzSimons (1932) does not occur in the area covered by this list. However, early records from British East Africa of the Senegalese species *trinodis* Boettger (1881), of which *schubotzi* Sternfeld (1917) is a synonym, may have been based on *mossambica*?

1841. *Rana Mascarcniensis* Duméril & Bibron, Erpét. Gén., **8**, p. 350: Madagascar; Mauritius; Seychelles.

1855. *Rana nilotica* Seetzen, Reise durch Syrien, Pälast., Aegypt, etc., **3**, p. 490: Egypt.

1857. *Rana savignyi* Jan, Cenni. Mus. Civ. Milano, p. 52 (probably Egypt, but this work is not available to me).

1864. ?*Rana idae* Steindachner, Verh. Zool.-Bot. Ges. Wien, **14**, p. 266, pl. xii, fig. 1: Madagascar.

1864. ?*Rana nigrescens* Steindachner, Verh. Zool.-Bot. Ges. Wien, **14**, p. 268, pl. xii, figs. 2 and 2a-2c: Madagascar.

1865. *Rana spinidactyla* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 197: Natal.

1881. *Rana abyssinica* Peters, Sitzb. Ges. Naturf. Freunde Berlin, p. 163: Ailet near Massawa; and Keren, Bogos, Eritrea.

1886. *Rana Newtonii* Bocage, Jorn. Sci. Lisboa, **11**, pp. 70, 73: São Tomé, Gulf of Guinea.

Range. *Egypt; *Sudan; *Ethiopia; *Uganda; *Kenya Colony; *Tanganyika Territory; *Zanzibar and Mafia Islands; *Madagascar; *Mozambique; *Nyasaland; *Northern and *Southern Rhodesia; *Transvaal; *Angola; *French Congo; *Nigeria; *Gold Coast; *Ivory Coast; *Liberia; *Sierra Leone.

Besides which it has been reported from almost every country in Africa, but due to confusion with closely related forms I have listed only those countries represented in the collection of the Museum of Comparative Zoology.

Rana mascareniensis venusta Werner

Primary-forest Mascarene-Frog

1908. *Rana venusta* Werner, Sitzb. Akad. Wiss. Wien, 1907, **116**, Abt. 1. pp. 1889, 1892, pl. iv, fig. 11: Mongala, Sudan; Entebbe, Uganda; Lagos, Nigeria.

Range. Primary or gallery forested areas of the southern Sudan; *Uganda; *Kenya Colony; *Tanganyika Territory, west through *Belgian Ruanda-Urundi and *Belgian Congo; *French and British Cameroon to Lagos, Nigeria.

Rana mascareniensis uzungwensis Loveridge

Montane Mascarene-Frog

1932. *Rana mascareniensis uzungwensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 384: Dabaga, Uzungwe Mountains, Tanganyika Territory.

1952. *Ptychadena macrocephala* Laurent, Revue Zool. Bot. Afr., **46**, p.

22: Upper Lubitshako River, 1900-2000 metres, south Kivu, Fizi Territory, Belgian Congo.

Range. Upland marshes of southern *Tanganyika Territory; *Nyasaland; *Southern Rhodesia; *Angola; Belgian Congo and Belgian Ruanda-Urundi.

Rana loveridgei (Laurent)[256]

1954. *Ptychadena loveridgei* Laurent, Ann. Mus. Roy. Congo Belge, **34**, p. 14, pl. i, fig. 4; pl. ii, fig. 1; pl. iii, figs. 3-4: Tare, Busanza, ca. 1800 metres, Astrida region, Belgian Ruanda-Urundi.

Range. Southwest Uganda; *Tanganyika Territory; Belgian Ruanda-Urundi; Belgian Congo; Angola.

Rana ansorgii Boulenger

1905. *Rana ansorgii* Boulenger, Ann. Mag. Nat. Hist., (7) **16**, p. 107, pl. iv, fig. 1: Between Benguela and Bihe, Angola.

Range. Southwest *Tanganyika Territory; Mozambique; *Nyasaland; *Northern Rhodesia; *Angola north to Lower Congo River and Katanga, Belgian Congo.

Rana fasciata merumontana Lönnberg

Northern Tanganyika Striped Grass-Frog

1907. *Rana merumontana* Lönnberg, in Sjöstedt, Wiss. Ergeb. Schwed. Zool. Exped. Kilimandjaro, Meru umgeb, Massaisteppen, No. 4, p. 21, pl. i, figs. 4a-b: Mount Meru, Tanganyika Territory.

Range. Montane meadows of northern *Tanganyika Territory.

Rana fasciata fülleborni Nieden

Southern Tanganyika Striped Grass-Frog

1910. *Rana fülleborni* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 436: Crater Lake, Ngosi Volcano, Poroto Mountains, Tanganyika Territory.

Range. Montane meadows of southern *Tanganyika Territory and *Nyasaland.

Rana stenocephala Boulenger Uganda Striped Grass-Frog

1901. *Rana stenocephala* Boulenger, Ann. Mag. Nat. Hist., (7) **8**, p. 515: Entebbe, Uganda.

Range. *Uganda (known only from the type locality).

[256] Whether this is a valid "species" remains to be seen; it is based in part on small ♂ paratypes of *R. m. uzungwensis* Loveridge (see above) from Dabaga and Kigogo, T. T. However, Laurent had abundant material and the countries given in the range are taken from his paratypes.

Rana occipitalis Günther Groove-crowned Bullfrog

1858. *Rana occipitalis* Günther, Cat. Batr. Sal. Brit. Mus., p. 130, pl. xi: Gambia; West Africa; Africa.

1863. *Rana hydraletis* "Boie" Peters (*nomen nudum*), Monatsb. Akad. Wiss. Berlin, p. 78: Type in Leiden Museum examined by Peters.

1864. *Rana bragantina* Bocage, Revue Mag. Zool. (2) **16**, p. 253: Duque de Braganca, Angola.

1924. *Ranosoma schereri* Ahl, Arch. Naturg., **90**, Abt. A, p. 250: Senegal.

1925. *Rana mwanzae* Loveridge, Proc. Zool. Soc. London, p. 772, pl. ii: Simiyu River at Sagayo, Mwanza Province, Tanganyika Territory.

1954. *Rana accidentalis* Lamotte & Zuber-Vogeli (*lapsus* for *occipitalis* Günther), Bull. Inst. Franc. Afr. Noire, **16**, Ser. A, p. 940.

Range. Reported from French Morocco; Algeria; Libya; *Sudan; Eritrea; *Uganda; Kenya Colony; *Tanganyika Territory; *Northern Rhodesia; Angola; Cabinda; *Belgian and French Congo; French Equatorial Africa; Sao Thomé; Fernando Po; *French and British Cameroon; Dahomey; Togo; *Gold Coast; *Liberia; *Sierra Leone; French and Portuguese Guinea; *Gambia; *Senegal.

Rana adspersa edulis (Peters) Eastern Burrowing-Bullfrog

1854. *Pyxicephalus edulis* Peters, Monatsb. Akad. Wiss. Berlin, p. 626: Boror; Tete; and Mozambique Island, Mozambique.

1893. *Phrynopsis Boulengerii* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 101, pl. ii, figs. 5-7: Mozambique.

1916. *Pyxicephalus flavigula* Calabresi, Monit. Zool. Ital. (Firenze), **27**, p. 34, pl. ii, fig. 1: Oroflillo, Somalia.

1924. *Phrynopsis usambarae* Ahl, Zool. Anz., **60**, p. 271: Usambara, Tanganyika Territory.

1927. *?Pyxicephalus obbianus* Calabresi, Atti Soc. Ital. Sci. Nat. (Milano), **66**, pp. 15, 35, pl. i, fig. 1: Dolobscio, near Obbia, Somalia.

Range. Somalia, south through *Kenya Colony; *Tanganyika Territory; *Mozambique; Nyasaland and Northern Rhodesia to the Zambezi River.[257]

Rana delalandii delalandii (Duméril & Bibron) Delaland's Burrowing-Frog

1841. *Pyxicephalus Delalandii* Duméril & Bibron, Erpét. Gén., **8**, p. 445, pl. lxxxvii, figs. 1 and 1a-b: South Africa.

[257] For detailed locality records, see Loveridge, 1950, Journ. E. Afr. Nat. Hist. Soc. for 1947-1948, **19**, pp. 253-255. The Museum of Comparative Zoology has typical *R. a. adspersa* (Tschudi) from Southern Rhodesia and the Transvaal, south to Cape Province.

1854. *Pyxicephalus marmoratus* Peters, Monatsb. Akad. Wiss. Berlin, p. 626: Boror, Mozambique.

1884. *Phrynobatrachus monticola* Fischer, Jahrb. Hamburg. Wiss. Anst., 1, p. 26: Southern Uaso Nyiro, Masailand, Kenya Colony.

1927. *Rana* (*Tomopterna*) *hieroglyphica* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 42: So. Omadu, Somalia.

1936. *Arthroleptis agadezi* Angel, Bull. Soc. Zool. France, **61**, p. 275: Agadez, Aïr, Sahara, French West Africa.

1938. *Arthroleptis ahli* Deckert, Sitzb. Ges. Naturf. Freunde Berlin, pp. 127, 168, fig. 46: Lichtenstein (approx. 32°50′ S., 26°E., between Bedford and Cheviot Falls, eastern Cape Province), South Africa.

1944. *Arthroleptis rosei* Hoffman, Soölog. Navors. Nas. Mus., Bloemfontein, 1, p. 174, figs. 1-4: "Chitiala," i.e. Chitala River, Nyasaland.

Range. Arid savanna regions in French West Africa (at Agadez: *fide* Guibé), west through the Sudan to Eritrea; south through *Ethiopia; *British Somaliland; *Somalia; Uganda; *Kenya Colony; *Tanganyika Territory; Mozambique; *Southern Rhodesia; Bechuanaland; *Transvaal; *Orange River; *Cape Province to Southwest Africa where it meets with the race *R. d. cryptotis* Boulenger.

Rana tuberculosa (Günther)[258] Angolan Burrowing-Frog

1864. *Pyxicephalus tuberculosa* Günther, Proc. Zool. Soc. London, p. 479, pl. xxxiii, fig. 1: Pungo Ndongo, Angola.

1896. *Rana pulchra* Boulenger, Ann. Mag. Nat. Hist., (6) **18**, p. 468: Lake Tanganyika (without indication as to which coast).

Range. "Lake Tanganyika;" Angola.

Rana ornata ornata (Peters)
Northern Ornate Burrowing-Frog

1878. *Pyxicephalus ornatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 207, pl. ii, fig. 7: "Taita," i.e. Teita, Kenya Colony.

1912. *Rana macrotympanum* Boulenger, Ann. Mag. Nat. Hist., (8) **10**, p. 140: West of Juba River, Gallaland, Ethiopia.

1919. *Rana* (*Hildebrandtia*) *togoensis* Boulenger,[259] Trans. Roy. Soc. S. Africa, **8**, p. 34: Mangu, Togo.

Range. Somalia; Kenya Colony; *Tanganyika Territory;

[258] Miss A. G. C. Grandison informs me (29.xi.56) that Boulenger himself synonymized *pulchra* with *tuberculosa* — of which we have only Angolan material. In details our frogs do not agree too well with the description of *pulchra*, and the relationship with *delalandii* requires investigation.

[259] New name for *H. ornatissima* Nieden (not of Bocage), proposed by Boulenger, sight unseen.

*Belgian Congo; French Equatorial Africa (det. A.L.); Togo; *Gold Coast.

Genus **PHRYNOBATRACHUS** Günther[260]

1849. *Stenorhynchus* A. Smith (not of Hemprich: 1820), Illus. Zool. S. Africa, Rept., App., p. 23. Type by monotypy: *S. natalensis* Smith.

1862. *Phrynobatrachus* Günther, Proc. Zool. Soc. London, p. 190. Type by monotypy: *P. natalensis* Günther (correct).

1863. *Leptoparius* Peters, Monatsb. Akad. Wiss. Berlin, p. 452. New name for *Stenorhynchus* A. Smith (preoccupied).

1925. *Hylarthroleptis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, 1923, p. 98. Type by present designation: *H. accraensis* Ahl.

1926. *Microbatrachus* Hewitt (not of Roux:1910), Ann. S. African Mus., **20**, p. 420. Type by original designation: *Phrynobatrachus capensis* Boulenger.

1926. *Microbatrachella* Hewitt, Ann. S. African Mus., **20**, p. 420, corrigenda slip. New name for *Microbatrachus* Hewitt (preoccupied).

Phrynobatrachus perpalmatus Boulenger

1898. *Phrynobatrachus perpalmatus* Boulenger, Proc. Zool. Soc. London, p. 479, pl. xxxviii, fig. 1: Lake Mweru, Northern Rhodesia.

1924. *Phrynobatrachus perpalmatus werneri* Ahl, Zool. Anz., **60**, p. 273: El Grassi, etc., Sudan.

Range. Sudan; *Tanganyika Territory; *Mozambique; *Nyasaland; *Northern Rhodesia; *Belgian Congo.

Phrynobatrachus acridoides (Cope)

1867. *Staurois acridoides* Cope, Journ. Acad. Nat. Sci. Philadelphia, **6**, p. 198: Zanzibar Island.

1919. *Phrynobatrachus Boulengeri* Witte, Revue Zool. Afr., **6**, p. 225: Beira and Coguna, Mozambique.

1923. *Hylarthroleptis medilineatus* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 100: "Tscharra, Danafluss," i.e. Charra, Tana River, Kenya Colony.

1923. *Hylarthroleptis janenschi* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 100: Tendaguru, near Lindi, Tanganyika Territory.

Range. Sudan; Eritrea; Somalia; *Kenya Colony; *Tan-

[260] Despite Hewitt's defense (1926, Ann. S. African Mus., **20**, p. 425) of the generic status of *Natalobatrachus* (Hewitt & Methuen, 1913, Trans. Roy. Soc. S. Africa, **3**, p. 107. Type by monotypy *N. boneberyi* Hewitt & Methuen) it should probably be regarded as a subgenus of *Phrynobatrachus* of which Noble regarded it as a synonym.

ganyika Territory;[261] Pemba, Zanzibar and Mafia Islands; Mozambique; Northern Rhodesia; French Equatorial Africa (*fide* Sternfeld:1917); *French and British Cameroon; also reported from Gold Coast (Witte:1919); French Guinea (Klaptocz:1913; Chabanaud:1921); Gambia (Witte:1919); Senegal (Mertens:1938).

Phrynobatrachus pakenhami Loveridge

1941. *Phrynobatrachus pakenhami* Loveridge, Proc. Biol. Soc. Washington, **54**, p. 178: Machengwe Swamp, near Wete, Pemba Island.

Range. Pemba Island.

Phrynobatrachus kinangopensis Angel

1924. *Phrynobatrachus Kinangopensis* Angel, Bull. Mus. Hist. Nat. (Paris), **30**, p. 130: Mount Kinangop, Aberdare Mountains, Kenya Colony.

Range. From 5000 (at Nairobi) to 11,000 feet (on Mount Kenya), in highlands of Kenya Colony.

Phrynobatrachus plicatus (Günther)

1858. *Hyperolius plicatus* Günther, Cat. Batr. Sal. Brit. Mus., p. 88, pl. vii, fig. C: Coast of Guinea.

1900. *Phrynobatrachus auritus* Boulenger, Proc. Zool. Soc. London, **2**, p. 440, pl. xxviii, fig. 2: Benito River, French Congo.

1919. *Phrynobatrachus discodactylus* Boulenger, Revue Zool. Afr., **7**, p. 7: "Madié," i.e. Medje, Ituri, Belgian Congo.

Range. *Uganda (Budongo Forest) and Belgian Ruanda-Urundi, west through *Belgian Congo to Cabinda, north and west through French Congo; Rio Muni; Fernando Po; *French and British Cameroon; Togo; Gold Coast; *Liberia to *Sierra Leone.

Phrynobatrachus krefftii Boulenger

1909. *Phrynobatrachus krefftii* Boulenger, Ann. Mag. Nat. Hist., (8) **4**, p. 496: Amani, Usambara Mountains, Tanganyika Territory.

Range. Usambara and Magrotto Mountains, Tanganyika Territory.[262]

[261] Frogs from the Uluguru Mountains of Tanganyika, referred with a query to *ogoensis* Boulenger by Barbour and Loveridge (1928), are referable to *acridoides*. The two species are so similar that one is inclined to doubt all West African records of "*acridoides*."

[262] Frogs from Ruwenzori and Ruanda-Urundi referred to *krefftii* by Nieden (1915) were subsequently renamed *versicolor* by Ahl (1924).

Phrynobatrachus dendrobates (Boulenger)

1919. *Arthroleptis dendrobates* Boulenger, Revue Zool. Afr., **7**, p. 8: "Madié," i.e. Medje, Ituri Forest, Belgian Congo.

1924. *Phrynobatrachus petropedetoides* Ahl, Zool. Anz., **61**, p. 102: Ruwenzori Mountains and west of Lake Edward, Belgian Congo.

Range. *Uganda; Belgian Ruanda-Urundi and the *Belgian Congo.[263]

Phrynobatrachus versicolor Ahl

1924. *Phrynobatrachus versicolor* Ahl, Zool. Anz., **61**, p. 100: Rugege Forest, Belgian Ruanda-Urundi.

Range. *Uganda; *Belgian Ruanda-Urundi and the *Belgian Congo.

Phrynobatrachus graueri (Nieden)

1910. *Arthroleptis graueri* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 441: Rugege Forest, Belgian Ruanda-Urundi.

Range. Western *Kenya Colony[264] and *Uganda, west through *Belgian Ruanda-Urundi to the *Belgian Congo.

Phrynobatrachus natalensis (Smith)

1849. *Sternorhynchus natalensis* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 24: Natal, South Africa.

1862. *Phrynobatrachus natalensis* Günther, Proc. Zool. Soc. London, p. 190: Natal, South Africa.

1862. *Dicroglossus angustirostris* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 341: Umvoti, Natal (by inference only).

1875. *Arthroleptis natalensis* var. *irrorata* Peters, Monatsb. Akad. Wiss. Berlin, p. 210: Accra, Gold Coast.

1894. *Phrynobatrachus ranoides* Boulenger, Proc. Zool. Soc. London, pp. 641, 644, pl. xxxix, fig. 2: Pietermaritzburg, Natal.

1904. *Phrynobatrachus natalensis* forma *gracilis* Andersson, Results Swed. Exped. Zool. to Egypt and the White Nile 1901, **1**, No. 4, p. 10, figs. —: Ghrab el Aish, south of Kaka on the White Nile, Sudan.

Range. *Sudan; Ethiopia; *Uganda; *Kenya Colony; *Tanganyika Territory; Zanzibar Island; Mozambique; *Nyasaland; *Northern and *Southern Rhodesia; Bechuanaland; *Transvaal; *Natal; Orange River; *Cape Province; Southwest Africa; *Angola; *Belgian Congo; Belgian Ruanda-Urundi; French

[263] The record from Accra, Gold Coast, of Deckert (1938), certainly requires verification.

[264] That is, Kaimosi and the Yala River region of Kakamega; the Mount Kinangop record of Angel (1925) is unacceptable.

Cameroon; Dahomey; Togo; *Liberia; *Sierra Leone; French Guinea; Portuguese Guinea; *Gambia; French West Africa.

Phrynobatrachus keniensis Barbour & Loveridge

1928. *Phrynobatrachus keniensis* Barbour & Loveridge, Proc. New England Zool. Club, **10**, p. 89: Mount Kenya, Kenya Colony.

Range. Upland meadows (Kikuyu; Molo; Mt. Kinangop; Mt. Kenya and Uplands) of Kenya Colony.

[**Phrynobatrachus bottegi** (Boulenger)]

1894. *Arthroleptis bottegi* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2) **15**, p. 16, pl. iv, fig. 3: Auata River, Somalia

Range. Ethiopia and Somalia.[265]

Phrynobatrachus minutus (Boulenger)

1895. *Arthroleptis minutus* Boulenger, Proc. Zool. Soc. London, p. 539, pl. xxx, fig. 4: "Durro," i.e. Duro, Ethiopia.

1910. *Arthroleptis scheffleri* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 438: Nairobi and Kibwezi, Kenya Colony; Mpwapwa, Tanganyika Territory; Zanzibar.

1924. *Arthroleptis albifer* Ahl, Arch. Naturg., **90**, Abt. A, p. 251: Usaramo, Tanganyika Territory.

Range. Sudan; Somalia; *Uganda; *Kenya Colony; *Tanganyika Territory; Zanzibar Island; *Northern Rhodesia; Transvaal (Mertens:1937); Angola (Monard:1937); *Belgian Congo. Also recorded from French Equatorial Africa (Sternfeld:1917); French Guinea (Chabanaud:1921) and Portuguese Guinea (Boulenger:1906), but all three require investigation.

Phrynobatrachus rungwensis (Loveridge)

1932. *Arthroleptis rungwensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 386: Ilolo, Rungwe Mountain, Tanganyika Territory.

Range. Southwestern *Tanganyika Territory and adjacent *Belgian Congo.[266]

[265] Records from Uganda (Peracca:1909; Boulenger:1911) and Belgian Congo (Noble:1924) require verifying. I examined the Kibongoto, T. T. specimens of Lönnberg (1907) and found they were based on *minutus* together with some juvenile *natalensis*. The record from Singida, T. T. (FitzSimons:1930) was also a juvenile *natalensis*.

[266] A series of frogs from Lukafu received from the Congo Museum as *gutturosus* Chabanaud, a species described from French Guinea.

Phrynobatrachus ukingensis mababiensis FitzSimons[267]

1932. *Phrynobatrachus mababiensis* FitzSimons, March, 1932, Ann. Transvaal Mus., **15**, p. 40, and 1935, *ibid.*, **16**, p. 390, fig. 26: Tsotsoroga Pan, Mababe Flats, Bechuanaland Protectorate.

1940. *Phrynobatrachus vanrooyeni* Hoffman, Soölog. Navors. Nas. Mus. Bloemfontein, **1**, p. 99, fig. 2B: Broedershoek, Greytown, Natal, South Africa.

1944. *Phrynobatrachus chitialaensis* Hoffman, Soölog. Navors. Nas. Mus. Bloemfontein, **1**, p. 177, figs. 5-6: "Chitiala," *i.e.* Chitala River, Nyasaland.

Range. Marshes, chiefly upland, of southern *Tanganyika Territory; Mozambique; *Nyasaland; *Northern Rhodesia; *Bechuanaland; *Natal; *Belgian Congo.

Phrynobatrachus ukingensis ukingenesis (Loveridge)

1932. *Arthroleptis ukingensis* Loveridge, Bull. Mus. Comp. Zool., **72**, p. 385: Madehani, Ukinga Mountains, Tanganyika Territory.

Range. Virgin forests of Ukinga and Rungwe Mountains, southern *Tanganyika Territory and Misuku Mountains, northern Nyasaland.

Phrynobatrachus rouxi (Nieden)

1912. *Arthroleptis rouxi* Nieden, Wiss. Ergebn. Deutsch. Zentral-Afrika-Exped. 1907-1908, **4**, p. 178, pl. v, figs. 5a-b: Northwest Buddu Forest, Uganda.

Range. Uganda and adjacent *Belgian Congo.[268]

Genus **ARTHROLEPTIS** Smith [269]

1849. *Arthroleptis* A. Smith, Illus. Zool. S. Africa, Rept., App., p. 24. Type by monotypy: *A. wahlbergii* Smith.

1863. *Hemimantis* Peters, Monatsb. Akad. Wiss. Berlin, p. 451. Type by monotypy: *H. calcaratus* Peters.

[267] Frogs from Nyamkolo, southeast end of Lake Tanganyika, Northern Rhodesia, topotypic of *moorii* Boulenger — to which I (1933) referred them in error — are referable to *mababiensis*. The extensive series from the Uzungwe, Ubena and Ukinga Mountains assigned by me (1933) to *parvulus* Boulenger, are also *mababiensis*, the description of which appeared only after my manuscript had gone to press. Subsequently I had the opportunity of examining the types of *moorii* and *parvulus* in the British Museum.

[268] The Mount Kenya record of Angel (1925) is considered doubtful.

[269] Laurent (1954, Ann. Mus. Congo, Zool., **1**, Misc. Zool. H. Schouteden, p. 35) presents a chart setting forth the osteological characters by which he separates *Schoutedenella*, at one end of the series, from *Arthroleptis*; his own (*Coracodichus* being intermediate between the extremes. His arrangement involves the transfer to *Schoutedenella* of at least a dozen *Arthroleptis*. The differences (doubtless with many minor variants yet to be discovered) are of such a nature that a subgeneric status appears to be the more logical way to escape the confusion arising from frequent transfer of species from one "genus" to another.

1921. *Schoutedenella* Witte, Revue Zool. Afr., **9**, p. 18. Type by monotypy: *S. globosa* Witte.

1925. *Pararthroleptis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, 1923, p. 98. Type by present designation: *P. nanus* Ahl.

1939. *Micrarthroleptis* Deckert, Sitzb. Ges. Naturf. Freunde Berlin, 1938, p. 166. Type by original designation: *Arthroleptis pygmaeus* Ahl.

1939. *Pseudarthroleptis* Deckert, Sitzb. Ges. Naturf. Freunde Berlin, 1938, p. 167. Type by original designation: "*Arthroleptis*," i.e. *Hemimantis calcaratus* Peters.

1940. *Abroscaphus* Laurent, Revue Zool. Bot. Afr., **34**, p. 82. Type by original designation: *Arthroleptis adolfifrederici* Nieden.

1940. *Coracodichus* Laurent, Revue Zool. Bot. Afr., **34**, p. 85. Type by original designation: *Arthroleptis whytii* Boulenger.

1940. *Arthroleptulus* Laurent, Revue Zool. Bot. Afr., **34**, p. 87. Type by present designation: *Arthroleptis xenodactylus* Boulenger (also included is the specimen of *xenodactyloides nkukae* misidentified as *A. schubotzi* by Loveridge).

Arthroleptis xenodactylus Boulenger[270]

1909. *Arthroleptis xenodactylus* Boulenger, Ann. Mag. Nat. Hist., (8) **4**, p. 496: Amani, Usambara Mountains, Tanganyika Territory.

1910. *Arthroleptis schubotzi* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 440: Usumbura, Belgian Ruanda-Urundi.

1954. *Schoutedenella sylvatica* Laurent, Ann. Mus. Congo, Zool., 1, Miscellanea Zool. H. Schouteden, p. 38: Buta, Uele, Belgian Congo.

Range. Forest floor from sea level to 6000 feet in *Tanganyika Territory; Belgian Ruanda-Urundi and the *Belgian Congo.

Arthroleptis xenodactyloides nkukae Loveridge

1942. *Arthroleptis xenodactyloides nkukae* Loveridge, Bull. Mus. Comp. Zool., **91**, p. 427: Nkuka Forest, Rungwe Mountain, Tanganyika Territory.

Range. Forest floor in the Uzungwe; Ukinga and Rungwe Mountains, southern *Tanganyika Territory.

Arthroleptis reichei Nieden

1910. *Arthroleptis reichei* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 437: Crater Lake, Ngosi Volcano, Poroto Mountains, Tanganyika Territory.

Range. Virgin forests of Uzungwe; Ukinga; Rungwe and

[270] I have compared topotypes of *xenodactylus* with topotypes (M.C.Z. 21718-21) of *sylvatica* from the original series collected by de Witte (in February, 1925) and see no justification for regarding *sylvatica* as distinct.

Poroto Mountains, southern *Tanganyika Territory and Misuku Mountains, northern *Nyasaland.

Arthroleptis poecilonotus Peters

1863. *Arthroleptis poecilonotus* "Schlegel" Peters, Monatsb. Akad. Wiss. Berlin, p. 446: Boutry, Ashanti, Gold Coast.

1882. *Arthroleptis macrodactylus* Boulenger, Cat. Batr. Sal. Brit. Mus., p. 117, pl. xi, fig. 5: Gabon, French Congo.

1885. *Arthroleptis bivittatus* F. Müller, Verh. Naturf. Ges. Basel, 7, p. 671, pl. ix, figs. k-l: Tumbo Island, French Guinea.

1900. *Arthroleptis inguinalis* Boulenger, Proc. Zool. Soc. London, p. 442, pl. xxvii, fig. 2: Benito River, Gabon, French Congo.

Range. Virgin forests of southern *Sudan; *Uganda[271]?; west through *Belgian and *French Congo; Fernando Po; *French and British Cameroon; *Nigeria; Dahomey; Togo; Gold Coast; *Ivory Coast; *Liberia; and *Sierra Leone to Portuguese Guinea.

Artholeptis adolfifriderici adolfifriderici Nieden[272]

1910. *Arthroleptis adolfi-friderici* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 440: Rugege Forest, Belgian Ruanda-Urundi.

1939. *Arthroleptis affinis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 303, fig. 1: (Type ♀ 39 mm.) Amani, Usambara Mountains, Tanganyika Territory.

1939. *Arthroleptis schoenebecki* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 305, fig. 2: (Type ♂ 22 mm.) Amani, Usambara Mountains, Tanganyika Territory.

Range. Virgin forests of (Mbololo Mountain) *Kenya Colony and (Usambara; Magrotto; Uluguru and Poroto Mountains) *Tanganyika Territory; west to Belgian Ruanda-Urundi and the *Belgian Congo.

Arthroleptis stenodactylus whytii Boulenger[273]

[271] Included on the basis of a not-too-well-preserved frog (M.C.Z. 25402) that I took at Mubango, Mabira Forest.

[272] Trinomials are employed because of a southeastern race (*A. a. francei* Loveridge:1953) occurring in Ruo River forest, Mlanje Mountain, Nyasaland.

[273] This montane-forest, burrow-breeding *Arthroleptis* differs from typical *s. stenodactylus* in having a metatarsal tubercle that is usually shorter than, though occasionally as long as, the inner toe; also the tibio-tarsal articulation of its forward-pressed hindlimb reaches the tympanum or, rarely, the eye. On the other hand, the lowland-savanna, burrow-breeding, *s. stenodactylus* has a metatarsal tubercle that is usually longer than the inner toe, though in juveniles it is occasionally only as long as the toe; the tibio-tarsal articulation of its adpressed hindlimb reaches only to the elbow or shoulder, very rarely as far as the tympanum.

Owing to the difficulty of separating juveniles, and the general similarity of the two forms, much confusion exists in the literature. *A. whytii* itself was a composite of the two races; *ulugurensis* was described by me owing to reliance on Ahl's advice when he said that my Uluguru frogs were not subspecifically identical with *lönnbergi* — of which I had no cotypes at that time. Now the Museum of Comparative Zoology has many topotypes of both *whytii* and all its synonyms.

1897. *Arthroleptis whytii* Boulenger, Proc. Zool. Soc. London, pp. 801, 802, pl. xlvi, fig. 3: "Masuka," i.e. Misuku Mountains, Nyasaland (restricted).

1915. *Arthroleptis lönnbergi* Nieden, Mitt. Zool. Mus. Berlin, **7**, p. 361: Mombo, foot of Usambara Mountains, Tanganyika Territory.

1932. *Arthroleptis stenodactylus uluguruensis* Loveridge, Proc. Biol. Soc. Washington, **45**, p. 61: Nyingwa, Uluguru Mountains, Tanganyika Territory.

1939. *Arthroleptis vagus* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 306: (Cotype ♂ 31 mm.; ♀ 38 mm.) Usambara Mountains, Tanganyika Territory.

1939. *Arthroleptis ukamiensis* Ahl, Sitzb. Ges. Naturf. Freunde Berlin, p. 308, fig. 3: (Type ♀ 33 mm.) Ukami, i.e. Uluguru Mountains, Tanganyika Territory.

Range. Virgin forests of Usambara; Magrotto; Uluguru; Rondo and Rungwe Mountains, *Tanganyika Territory; also Misuku; Nchisi; Mlanje and Cholo Mountains, *Nyasaland; Mozambique and Chirinda Mountain, *Southern Rhodesia.[274]

Arthroleptis stenodactylus stenodactylus Pfeffer[275]

1893. *Arthroleptis stenodactylus* Pfeffer, Jahrb. Hamburg. Wiss. Anst., 1892, **10**, p. 93, pl. i, fig. 2: Kihengo, Tanganyika Territory.

1924. *Arthroleptis methneri* Ahl, Arch. Naturg., **90**, Abt. A, p. 251: Nangoma Cave, Matumbi near Kilwa, Tanganyika Territory.

1927. ?*Arthroleptis elegans* Calabresi, Atti Soc. Ital. Sci. Nat. (Milano), **66**, pp. 16, 35: Hongolo, Uadi Hoor, Somalia.

Range. Dry savanna, chiefly on the coastal plain, of *Kenya Colony; *Tanganyika Territory; Mozambique; *Nyasaland; *Northern Rhodesia; *Belgian Congo.[276]

Genus **CACOSTERNUM** Boulenger

1887. *Cacosternum* Boulenger, Ann. Mag. Nat. Hist., (5) **20**, p. 51. Type by monotypy: *C. nanum* Boulenger.

[274] Credibly reported from the Belgian Congo by de Witte (1934), though possibly typical *stenodactylus* of which we have examples from Kanyama, B. C.

[275] *A. elegans*, described from four 19 mm. frogs, is tentatively listed in the synonymy in the hope that someone, bearing in mind the possibility they may be juvenile *s. stenodactylus*, will restudy the material.

[276] Also reported from French Cameroon and Sierra Leone by Angel (1940), possibly owing to confusion with *variabilis* Matschie.

Cacosternum boettgeri boettgeri (Boulenger)[277]

1882. *Arthroleptis boettgeri* Boulenger, Cat. Batr. Sal. Brit. Mus., p. 118, pl. xi, fig. 6: Vleis, Kaffraria, Bechuanaland Protectorate.

1887. *Cacosternum nanum* Boulenger, Ann. Mag. Nat. Hist., (5) **20**, p. 52: Vleis, Kaffraria, Bechuanaland Protectorate.

1914. *Arthroleptis schebeni* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, 1913, p. 438: Klein Nauas, Southwest Africa.

Range. Occurs in both upland savanna and arid regions of East Africa, viz. Somalia; *Uganda; *Kenya Colony; Bechuanaland Protectorate; *Transvaal; Natal (? and/or the race *albiventer* Hewitt); *Orange River; Basutoland; *Cape Province; *Southwest Africa.

Genus **HEMISUS** Günther

1858. *Hemisus* Günther, Cat. Batr. Sal. Brit. Mus., p. 47. Type by monotypy: *Engystoma guttatum* Rapp.

1863. *Kakophrynus* Steindachner, Sitzb. Akad. Wiss. Wien, **48**, Abt. 1, p. 191. Type by monotypy: *K. sudanesis* (*sic*) Steindachner = *Engystoma marmoratum* Peters.

Hemisus marmoratus marmoratus (Peters)

Eastern Sharp-snouted Frog

1854. *Engystoma marmoratum* Peters, Monatsb. Akad. Wiss. Berlin, p. 628: Cabaceira, Mozambique.

1863. *Kakophrynus sudanesis* (*sic*) Steindachner, Sitzb. Akad. Wiss. Wien, **48**, Abt. 1, p. 191, pl. i, figs. 10-13: Sudan.

1882. *Hemisus taitanus* Peters, Reise nach Mossambique, **3**, p. 175: "Taita," i.e. Teita, Kenya Colony.

Range. *Sudan; Eritrea; *Kenya Colony; *Tanganyika Territory; Zanzibar Island; *Mozambique; *Nyasaland; Southern Rhodesia; Bechuanaland Protectorate; *Transvaal; southeast Belgian Congo (Angola records are presumably referable to the western race).

[277] From Kundelungu Plateau research station at 1750 metres, in Katanga, southeast Belgian Congo, Laurent (1950, Revue Zool. Bot. Afr., **44**, p. 138) has described a single 14 mm. frog as *C. lelcupi*. It is said to differ from *boettgeri* by (1) lacking maxillary teeth; (2) by the absence of markings on its hindlimbs. It is true that limb markings are present in our extensive representation of *boettgeri* from southern Africa. In East Africa, however, markings are both present (M.C.Z. 25478 — 3 ex.) and absent (M.C.Z. 25479 — 2 ex.) in a series from Kinangop Plateau (11,000 feet). In another Kinangop series markings are present in 17 frogs, absent in 3 (M.C.Z. 16104, 16107, 16109). My colleague Dr. E. E. Williams finds maxillary teeth present in all sizes of those he has examined.

Hemisus marmoratus guineensis Cope

Western Sharp-nosed Frog

1865. *Hemisus guineensis* Cope, Nat. Hist. Review, **5**, p. 100, footnote. Type in Vienna Museum: Guinea (by inference).

1882. *Engystoma vermiculatum* "Schlegel" Peters, Reise nach Mossambique, **3**, p. 175: Ashanti, Gold Coast.

Range. *Western Tanganyika Territory; Angola; *Belgian Congo; French Congo; French Equatorial Africa; *French Cameroon; Nigeria; Dahomey; *Gold Coast; *Liberia; *Sierra Leone; French Guinea; Portuguese Guinea; Gambia; Senegal.

Family PHRYNOMERIDAE[278]

Genus **PHRYNOMERUS** Noble

1847. *Brachymerus* A. Smith (not of Dahlbom:1845), Illus. Zool. S. Africa, Rept., text to pl. lxiii. Type by monotypy: *B. bifasciatus* A. Smith.

1926. *Phrynomerus* Noble, Amer. Mus. Novit., No. 237, p. 20. New name for *Brachymerus* A. Smith (preoccupied).

Phrynomerus bifasciatus bifasciatus (Smith)

1847.[279] *Brachymerus bifasciatus* A. Smith, Illus. Zool. S. Africa, Rept., pl. lxiii: "Country to the east and north-east of Cape Colony," i.e. east of Cape Province, South Africa.

1849.[280] *Dendrobates inhambanensis* Bianconi (1848), Nuovi Ann. Sci. Nat., (2) **10**, p. 107, pl. v, figs. 4-4a; also 1850, Spec. Zool. Mosamb., Rept., p. 26, pl. v. figs. 4-4a: Inhambane, Mozambique.

1944. *Phrynomerus bifasciatus nyasalandensis* Hoffman, Soölog. Navors. Nas. Mus. Bloemfontein, **1**, p. 181, fig. 9: "Chitiala," i.e. Chitala River, Nyasaland.

[278] The status of the African genus *Phrynomerus* has been a chequered one. In 1858 (as *Brachymerus*) it was made the type of a family (BRACHYMERIDAE) by Günther (Cat. Batr. Sal. Brit. Mus., p. 124), only (as *Phrynomantis*) to be merged in the family ENGYSTOMATIDAE by Boulenger (1882, Cat. Batr. Sal. Ecaud. Brit. Mus., p. 172). In 1931 (as *Phrynomerus*) it was given subfamily rank (PHRYNOMERINAE) in the BREVICIPITIDAE by Noble (Biology of the Amphibia, p. 538), later to be raised to full family status (PHRYNOMERIDAE) by Parker (1934: Monograph of the Frogs of the Family MICROHYLIDAE, p. 9) principally on account of its intercalary phalanges, a character it shares with the RHACOPHORIDAE.

For other ways in which PHRYNOMERIDAE differs or agrees with MICROHYLIDAE, together with a lucid tabulation of the characteristics of all African firmisternal families, see Parker (*loc. cit.* pp. 8-9).

[279] Actually appeared in December, 1847, *fide* Waterhouse (1880, Proc. Zool Soc. London, p. 490).

[280] Bianconi subsequently claimed that this description first appeared on February 4, 1847, in Mem. Accad. Sci. Ist. Bologna, **1**, p. 498 (a publication not available to me).

Range. Kenya Colony; Tanganyika Territory; Zanzibar and Mafia Islands; south to Zululand; west to Cape Province; northwest through Southwest Africa to Angola and the Belgian Congo.[281]

Family MICROHYLIDAE[282]

Genus **CALLULINA** Nieden

1910. *Callulina* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 449. Type by monotypy: *C. kreffti* Nieden.

Callulina kreffti Nieden

1910. *Callulina kreffti* Nieden, Sitzb. Ges. Naturf. Freunde Berlin, p. 449: Amani, Usambara Mountains; and Tanga, Tanganyika Territory.

Range. Usambara, Magrotto and Uluguru Mountains, Tanganyika Territory.

Genus **SPELAEOPHRYNE** Ahl

1924. *Spelaeophryne* Ahl, Zool. Anz., **61**, p. 99. Type by original designation: *S. methneri* Ahl.

Spelaeophryne methneri Ahl Scarlet-snouted Black Frog

1924. *Spelaeophryne methneri* Ahl, Zool. Anz., **61**, p. 99: Nangoma Cave, Matumbi near Kilwa, Tanganyika Territory.

Range. Eastern Tanganyika Territory.

Genus **PROBREVICEPS** Parker

1931. *Probreviceps* Parker, Ann. Mag. Nat. Hist., (10) **8**, p. 262. Type by original designation: *Breviceps macrodactylus* Nieden.

Probreviceps macrodactylus macrodactylus (Nieden)

1926. *Breviceps macrodactylus* Nieden, Das Tierreich, **49**, Anura, **2**, p.

[281] The western race *microps* Peters, has been reported from the Belgian Congo, Sudan and the *Gold Coast (M.C.Z.).

[282] This name, originally spelled MICRHYLIDAE by Günther (1858, Cat. Batr. Sal. Brit. Mus., p. 121), was amended and used by Parker (1943, Monograph of the Frogs of the Family MICROHYLIDAE) for the family that, following Noble, I have hitherto consistently called BREVICIPITIDAE of Cope (part). It is typified by *Rana gibbosa* Linnaeus = *Breviceps gibbosus* (Linnaeus), the only member of the family known to him in 1758.

The argument for retaining BREVICIPITIDAE advanced by Dunn (1935. Copeia, p. 108) appears to be fallacious, being based on a misconception of Parker's reasons for selecting *MICROHYLIDAE*. It is necessary only to add that the sole species included by Günther in his MICRHYLIDAE was *Microhyla achatina* Tschudi of Java.

6: Usambara Mountains, Tanganyika Territory.

1928. *Breviceps usambaricus* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 251: Amani, Usambara Mountains, Tanganyika Territory.

Range. Usambara Mountains, Tanganyika Territory.

Probreviceps macrodactylus loveridgei Parker

1931. *Probreviceps macrodactylus loveridgei* Parker, Ann. Mag. Nat. Hist., (10) **8**, p. 263: Bagilo, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains, Tanganyika Territory.

Probreviceps macrodactylus rungwensis Loveridge

1932. *Probreviceps macrodactylus rungwensis* Loveridge, Bull. Mus. Comp Zool., **72**, p. 387: Nkuka Forest, Rungwe Mountain, Tanganyika Territory.

Range. Rungwe Mountain, Tanganyika Territory.

Probreviceps uluguruensis (Loveridge)

1925. *Breviceps uluguruensis* Loveridge, Proc. Zool. Soc. London, p. 789, pl. i, fig. 3: Bagilo, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains, Tanganyika Territory.

Genus **BREVICEPS** Merrem

1820. *Breviceps* Merrem, Vers. Syst. Amphib., p. 177. Type by monotypy: *Rana gibbosa* Linnaeus.

1826. *Engystoma* Fitzinger, Neue Class. Rept., pp. 39, 65. Type by original designation: *Rana gibbosa* Linnaeus.

1830. *Systoma* Wagler, Nat. Syst. Amphib., p. 205. Type by monotypy: *Breviceps gibbosus* Merrem = *Rana gibbosa* Linnaeus.

Breviceps mossambicus Peters Mozambique Short-headed Frog

1829. *Engystoma granosum* Cuvier (*nomen nudum*), Règne Animal, ed. 2, **2**, p. 112: "Cap," i.e. South Africa; probably Natal.

1854. *Breviceps mossambicus* Peters, Monatsb. Akad. Wiss. Berlin, p. 628: Mozambique Island, and Sena, Mozambique.

1944. *Breviceps mitchelli* Hoffman, Soölog. Navors. Nas. Mus. Bloemfontein **1**, p. 182, fig. 10: "Chitiala," i.e. Chitala River, Nyasaland.

Range. Tanganyika Territory, south to Natal, northwest through Southern Rhodesia to Angola and the Belgian Congo.

Genus **PARHOPLOPHRYNE** Barbour & Loveridge

1928. *Parhoplophryne* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 260. Type by original designation: *P. usambaricus* (*sic*) Barbour & Loveridge.

Parhoplophryne usambarica Barbour & Loveridge

1928. *Parhoplophryne usambaricus* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 260: Amani, Usambara Mountains, Tanganyika Territory.

Range. Usambara Mountains, Tanganyika Territory.

Genus **HOPLOPHRYNE** Barbour & Loveridge

1928. *Hoplophryne* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 253. Type by original designation: *H. uluguruensis* Barbour & Loveridge.

Hoplophryne rogersi Barbour & Loveridge
Usambara Banana-Frog

1928. *Hoplophryne rogersi* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 258, pl. ii, fig. 5: Mount Bomoli, Amani, Usambara Mountains, Tanganyika Territory.

Range. Usambara and Magrotto Mountains, Tanganyika Territory.

Hoplophryne uluguruensis Barbour & Loveridge
Uluguru Banana-Frog

1928. *Hoplophryne uluguruensis* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 254, pl. ii, figs. 3-4: Mount Mbova, Nyange, Uluguru Mountains, Tanganyika Territory.

Range. Uluguru Mountains, Tanganyika Territory.

LIST OF SPECIES OR RACES STILL UNREPRESENTED IN THE MUSEUM OF COMPARATIVE ZOOLOGY, CAMBRIDGE

LIZARDS

**Hemidactylus albopunctatus* Loveridge	Haud, British Somaliland
Ebenavia sp.	Chokocho, Pemba Island
Chamaeleo bitaeniatus schubotzi Sternfeld	Mt. Kenya at 14,000 feet
Chamaeleo fischeri uthmolleri L. Müller	Mt. Hanang at 2,300 feet
Chamaeleo fischeri fischeri Reichenow	Mt. Nguru, Tang. Terr.
Mabuya varia brauni Tornier	Ukinga Mtns., Tang. Terr.
Lygosoma kutuensis Lönnberg	Kutu Village nr Fort Hall, K.C.
**Philochortus intermedius rudolfensis* Parker	Kaliokwell River, K.C.
Ichnotropis tanganicana Boulenger	Lake Tanganyika

SNAKES

**Leptotyphlops fiechteri* Scortecci	Duke of Abruzzi's Villa, Somalia
**Telescopus dhara somalicus* (Parker)	Ngatana, Tana River, K.C.
Crotaphopeltis werneri Boulenger	Usambara Mountains, Tang. Terr.
Calamelaps unicolor polylepis Bocage	Tukuyu, s.w. Tang. Terr.

TOADS AND FROGS

**Bufo regularis marakwetensis* Roux	Mt. Marakwet at 2500 m., K.C.
Bufo lindneri Mertens	Dar es Salaam, Tang. Terr.
**Leptopelis gramineus* (Boulenger)	Badditu to Dime, Somalia
Hylambates verrucosus Boulenger	Mabira Forest, Kyagwe, Uganda
Hyperolius albifrons Ahl	"Africa" Mafia Island, T.T.
Hyperolius albofrenatus Ahl	Tanganyika Territory
Hyperolius albolabris Ahl	Kwa Buosch or Bnorch, T.T.
Hyperolius bergeri Ahl	Uaso Narok, Kenya Colony
Hyperolius glandicolor Peters	Teita, Kenya Colony
Hyperolius guttolineatus Ahl	Tanganyika Territory
Hyperolius marmoratus campylogrammus Laurent	Bura, 1050 m., Teita, K.C.
**Hyperolius pachydermus* Werner	Gondokoro, Sudan; also U.; K.C.

Hyperolius pantherinus (Steindachner)	Laikipia, Kenya Colony
Hyperolius quadratomaculatus Ahl	Mohoro, Tanganyika Territory
Hyperolius scriptus Ahl	Tanga, Tanganyika Territory
Hyperolius tornieri Ahl	Uluguru Mountains, T.T.
Hyperolius viridiflavus pitmani Laurent	Lake Bunyoni, s.w. Uganda
Phrynobatrachus bottegi (Boulenger)	Auata River, Somalia
Phrynobatrachus rouxi Nieden	N.W. Buddu Forest, Uganda

ANNOTATED BIBLIOGRAPHY

of revisionary studies or other contributions likely to be useful to anyone taking up the study of East African herpetology. Those selected have all been published since G. A. Boulenger's nine-volume series of catalogues on the collections in the British Museum (1882-1896).

BOULENGER, G. A.

1915. A List of the Snakes of East Africa, north of the Zambesi and south of the Soudan and Somaliland, and of Nyassaland. Proc. Zool. Soc. London, pp. 611-640, figs. 1-3. (Still the handiest aid to an *approximate* identification of most snakes, though the nomenclature is even more obsolete than the spelling of Zambezi, Sudan and Nyasaland.)

1920-1921. Monograph of the Lacertidae. (British Museum), **1**, pp. x + 352; **2**, pp. viii + 451. (Contains good descriptions of most of the 21 East African forms, but the nomenclature is binomial; geographical races are treated either as full species or "varieties," a term variously employed.)

LAURENT, RAYMOND

1950. Revision du genre *Atractaspis* A. Smith. Mem. Inst. Roy. Sci. Nat. Belgique, (2) **38**, pp. 1-49, figs. 1-18. (This well-illustrated treatise subdivides somewhat excessively; see footnotes to pp. 296-297 of this check list regarding the East African forms.) See also G. F. de Witte and R. Laurent.

LOVERIDGE, ARTHUR

1923. A List of the Lizards of British Territories in East Africa . . . with Keys for the Diagnosis of the Species. Proc. Zool. Soc. London, pp. 841-863. (Moderately serviceable where not replaced by family revisions, as listed below.)

*An asterisk indicates that it occurs in the Northern Frontier Province of Kenya Colony.

The Museum of Comparative Zoology would be glad to offer an exchange for examples of any of the foregoing 32 desiderata.

1924. Check List of the Reptilia recorded from the British Territories in East Africa. Journ. E. Africa Uganda Nat. Hist. Soc. Spec. Suppl., No. 3, pp. 1-16. (Superseded.)

1930. A List of the Amphibia of the British Territories in East Africa . . . with Keys for the Diagnosis of the Species. Proc. Zool. Soc. London, pp. 7-32. (Rather useless; as at least 40 species have been added, and some removed, since 1930.)

1939. Revision of the African Snakes of the Genera *Mehelya* and *Gonionotophis*. Bull. Mus. Comp. Zool., **86**, pp. 131-162, figs. 1-2. (Substantially up to date; some range extensions.)

1940. Revision of the African Snakes of the Genera *Dromophis* and *Psammophis*. Bull. Mus. Comp. Zool., **87**, pp. 1-70. (No change as regards East African forms, but some workers disapprove of *schokari* and certain southwestern snakes being treated as races of *sibilans*.)

1941. Revision of the African Lizards of the Family Amphisbaenidae. Bull. Mus. Comp. Zool., **88**, pp. 467-524, figs. 1-53. (See footnote to *Amphisbaena* in this check list.)

1941. Revision of the African Terrapin of the Family Pelomedusidae. Bull. Mus. Comp. Zool., **88**, pp. 467-524. (The West African *Pelusios niger* should be removed from the synonymy of *subniger*.)

1942. Revision of the Afro-Oriental Geckos of the Genus *Phelsuma*. Bull. Mus. Comp. Zool., **89**, pp. 437-482, figs. 1-2, map.

1942. Revision of the African Lizards of the Family Gerrhosauridae. Bull. Mus. Comp. Zool., **89**, pp. 483-543. (Now merged with the Cordylidae.)

1944. Revision of the African Lizards of the Family Cordylidae. Bull. Mus. Comp. Zool., **95**, pp. 1-118, pls. i-xii. (See also Gerrhosauridae above.)

1944. Further Revisions of African Snake Genera. Bull. Mus. Comp. Zool., **95**, pp. 119-247. (Deals with *Rhamnophis; Thrasops; Duberria; Thelotornis; Calamelaps; Miodon; Aparallactus; Elapsoidea* and *Paranaja*.)

1947. Revision of the African Lizards of the Family Gekkonidae. Bull. Mus. Comp. Zool., **98**, pp. 1-469, pls. i-vii. (This revision, like its predecessors, contains keys to the species together with a synopsis of all that is known of their life history, enemies, parasites, etc.)

LOVERIDGE, A., and E. E. WILLIAMS

1957. Revision of the African Tortoises and Turtles of the Suborder Cryptodira. Bull. Mus. Comp. Zool., **115**, pp. 163-557, figs. 1-62, pls. i-xviii. (Together with the revision of the Pelomedusidae, Suborder Pleurodira, this covers all the African Testudinata.)

MERTENS, ROBERT

1942. Die Familie der Warane (Varanidae), III. Taxonomie. Abhand. Senckenberg. Naturf. Ges., No. 466, pp. 237-391. (Nos. 462 and 465, the first two parts of this exhaustive treatise by a foremost herpetologist, deal with the skull, etc. etc. They also appeared in 1942.)

MERTENS, ROBERT and HEINZ WERMUTH

1955. Die rezenten Schildkröten, Krokodile und Brückenechsen. Zool. Jahrb., Syst., **83**, pp. 323-440. (A check list of the turtles, tortoises, crocodiles and tuatara of the world.)

MOREAU, R. E. and R. H. W. PAKENHAM

1941. The Land Vertebrates of Pemba, Zanzibar, and Mafia: a Zoogeographical Study. Proc. Zool. Soc. London for 1940, **110** (A), pp. 97-128, fig. 1.

1942. Corrigenda and Addenda to "The Land Vetebrates of Pemba, Zanzibar, and Mafia: a Zoogeographical Study." Proc. Zool. Soc. London, **112**, (A), pp. 61-63.

PAKENHAM, R. H. W., see R. E. MOREAU and R. H. W. PAKENHAM

PARKER, H. W.

1934. A Monograph of the Frogs of the Family Microhylidae. London, pp. viii + 208, figs. 1-67.

PITMAN, C. R. S.

1938. A Guide to the Snakes of Uganda. (Kampala), pp. xxi + 362, pls. i-xxviii, col. pls. A-Q, diagrams I-II, maps. (The excellent figures and coloured plates make this work invaluable to beginners. A new and revised edition is in course of preparation as the 1938 edition is out of print.)

WILLIAMS, ERNEST E., see A. LOVERIDGE and E. E. WILLIAMS

WITTE, G. F. DE, and R. LAURENT

1943. Contribution à la Systématique des Formes dégradés de la Famille des Scincidae apparentées au Genre *Scelotes* Fitzinger. Mém. Mus. Roy. Hist. Nat. Belgique, (2) **20**, pp. 1-44, figs. 1-61.

1947. Revision d'un Groupe de Colubridae Africains (Genres *Calamelaps, Miodon, Aparallactus* et Formes affines). Mém. Mus. Roy. Hist. Nat. Belgique, (2) **29**, pp. 1-134, figs. 1-132. (The conclusions arrived at by these authors are often at variance with those in my 1944 paper dealing with the same genera. A.L.)

INDEX

To reduce the bulk of this index, specific or racial names have not been listed under the heading of the genera to which they belong but only individually as species or races. To find all the "East African" species represented in any given genus it will be necessary to turn to the genus in question in the text.

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THE SPIDER GENERA *CRUSTULINA* AND *STEATODA* IN NORTH AMERICA, CENTRAL AMERICA, AND THE WEST INDIES (ARANEAE, THERIDIIDAE)

By Herbert W. Levi

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No. 3—*The Spider Genera* Crustulina *and* Steatoda *in North America, Central America, and the West Indies (Araneae, Theridiidae).*

By Herbert W. Levi

This paper is one of the last in a series of generic revisions in the family Theridiidae of North America, Central America and the West Indies.

The genera revised in this paper are characterized by having a large colulus between the anterior spinnerets, lacking teeth on the posterior margin of the chelicerae, and having the lateral eyes close to each other or touching.

The spiders here placed in *Steatoda* have previously been distributed among four genera: *Asagena, Lithyphantes, Steatoda* and *Teutana.* The characters which have been used to separate the four genera are no longer useful as they are based on the limited European fauna. The *Steatoda* of previous authors was characterized by having the anterior median eyes larger than the others; however, several species placed in *Lithyphantes* may have individuals with anterior median eyes the largest (*S. medialis; S. pulcher*). *Lithyphantes* has been characterized as having the lateral eyes slightly separated from each other; however, this character is also present in *Steatoda,* while in some species of *Lithyphantes,* the lateral eyes touch. The few species of *Teutana* have the eyes subequal in size and the lateral eyes touching each other, a combination of characters hardly different from that found in many *Lithyphantes* species. Several species placed in *Lithyphantes* had their opposite sexes described in *Asagena.* The shape of the labium and the shape of the sternum are unreliable characters. The latter depends in part on the size of the spider; the former is a characteristic of individual species. The carapace is narrow and long in some, usually the smaller, species; almost as wide as long in the largest. In several species of *Lithyphantes,* the paracymbial hook is on the mesal side in the cymbium of the male palpus; in others placed in *Lithyphantes,* and in species previously placed in *Steatoda* and *Teutana,* it is on the ectal side. However, no sharp line

can be drawn here either; there are species which are intermediate.

The idea that some of these genera ought to be combined is not new. Emerton placed species of *Teutana* in *Steatoda*. F.O.P. Cambridge (1902, Biologia Centrali Americana, Araneidea, vol. 2, p. 374) wrote that "The spiders referred to this genus [*Teutana*] are very difficult to separate by any reliable character from those included under *Lithyphantes,* though as far as one can judge, from the material at hand, the contiguity of the lateral eyes may prove constant." We now know that this latter character did not prove constant. Other authors also have commented on the difficulty of separating these genera.

This revision is based on material in the Museum of Comparative Zoology. Dr. W.J. Gertsch has made available to me the large collections of the American Museum of Natural History, for which I would like to thank him. Other collections were made available by Dr. A.M. Chickering; Mrs. D. Frizzell (Dr. H. Exline); Mr. V. Roth; Mr. R.X. Schick; and Dr. R.V. Chamberlin sent specimens of the *Steatoda bipunctata* group. Mr. Schick has raised male *Steatoda palomara* to maturity, making it possible to figure its palpus for the first time. Mr. E. Browning of the British Museum (Natural History) sent a syntype of *Steatoda americana* O.P. Cambridge, and a palpus of the type of *Lithyphantes quaesita,* as well as other specimens. Dr. H. Wiehle of Dessau has sent some male *Steatoda castanea* from Germany. I wish to express my sincere thanks for the cooperation of these colleagues.

The bibliographies of holarctic and cosmopolitan species are not complete; if needed, they can be consulted in Roewer's recent Katalog or in Bonnet's Bibliographia.

The drawings of palpi illustrate the left ones. Although keys are usually not necessary to determine spiders to species, two keys are included to point out differences in genitalia of the two species groups of *Steatoda.*

Crustulina Menge

Crustulina Menge, 1868, Schr. Naturf. Gesell. Danzig, new ser., vol. 2, p. 168. Type species: *Crustulina guttata* (Wider).

Description. Small theridiid spiders (1-3 mm. total length).

Carapace longer than wide. Carapace and sternum covered by large elongate dark tubercles, which are the bases of fine hairs. Anterior eye row procurved, posterior slightly recurved. Eyes subequal in size. Anterior median eyes their diameter apart, almost touching laterals. Posterior medians one diameter apart, one diameter or slightly less from laterals. Height of clypeus equals three to four diameters of anterior medians in female, four to five diameters in male. Chelicerae with one large tooth on anterior margin, posterior margin without teeth. Legs relatively short, first or fourth legs longest, third shortest. A tarsal comb present on fourth tarsus. Abdomen subspherical, slightly flattened dorso-ventrally. Colulus large. Sclerotized ridge on anterior end of abdomen of males, as in *Steatoda,* but this structure also present in females.

Genitalia. Epigynum illustrated by Figures 2 and 5. Palpus with usual structures (Fig. 9); however, cymbium has a mesal process which may be homologous to the paracymbial hook in other genera.

Diagnosis. This genus differs from most theridiid genera by having a large colulus, and lacking teeth on the posterior margin of the chelicerae; it differs from *Steatoda* in having large dumb-bell shaped tubercles on carapace and sternum, in having a sclerotized ring around the pedicel on the abdomen of females and in having a median distal process on the cymbium of the male palpus.

Remarks. Since many species placed in *Crustulina* probably do not belong to it, its distribution is difficult to judge. *Crustulina lascivula* Keyserling, (1886, Die Spinnen Amerikas, vol. 2, pt. 2, p. 39, pl. 12, fig. 155, ♀), is *Paidisca unimaculata* (Emerton).

Crustulina guttata (Wider)

Theridion guttatum Wider, 1834, Abhandl. Mus. Senckenberg, vol. 1, p. 241, pl. 16, fig. 7, ♀, ♂.

Crustulina guttata, Wiehle, 1937, in Dahl, Die Tierwelt Deutschlands, pt. 33, p. 191, figs. 194-199, ♀, ♂. Locket and Millidge, 1953, British spiders, vol. 2, p. 51, figs. 26d, 35a,b,e, ♀, ♂.

This species has not been found in America. The many American references to the name *Crustulina guttata* are actually

either *C. altera* or *C. stricta*. Both are very similar to it, and only details of the genitalia distinguish *C. guttata*.

Crustulina sticta (O.P. Cambridge)

Figures 1-3, 7; Map 1.

Theridion stictum O.P. Cambridge, 1861, Ann. Mag. Nat. Hist., ser. 3, vol. 7, p. 432. Emerton, 1876, Psyche, vol. 1, p. 129; 1877, Proc. Boston Soc. Nat. Hist., vol. 19, p. 70.

Steatoda sticta, Thorell, 1873, Remarks on synonyms of European spiders, p. 439.

Crustulina sticta, Simon, 1881, Les Arachnides de France, vol. 5, p. 158. Banks, 1895, Ann. New York Acad. Sci., vol. 8, p. 417; 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus.

Map 1. American distribution of *Crustulina sticta* (O.P. Cambridge).

Nat. Hist., vol. 29, p. 172. Crosby and Bishop, 1928, Mem. Cornell Agr. Exp. Sta., no. 101, p. 1039. Emerton, 1930, Publ. Nantucket Maria Mitchell Assoc., vol. 3, p. 164. Roewer, 1942, Katalog der Araneae, vol. 1, p. 399. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 75, figs. 34, 2120, ♀, ♂. Locket and Millidge, 1953, British spiders, vol. 2 p. 53, figs. 35d,e,f, ♀, ♂. Kaston, 1955, Trans. Illinois Acad. Sci., vol. 45, p. 166. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 1256.

Crustulina borealis Banks, 1900, Canadian Ent., vol. 32, p. 98; 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 172. Emerton, 1920, Trans. Roy. Canadian Inst., vol. 12, p. 312. Worley, 1932, Publ. Univ. Washington Biol., vol. 1, p. 23. Roewer, 1942, Katalog der Araneae, vol. 1, p. 399; Gertsch, 1946, *in* Procter, Biol. Surv. Mt. Desert Reg., pt. 7, p. 519. Chamberlin and Ivie, 1947, Bull. Univ. Utah, biol. ser., vol. 10, no. 3, p. 25. Hackman, 1954, Acta Zool. Fennica, vol. 79, p. 48. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 1252.

Crustulina pallipes Banks, 1906, Proc. Ent. Soc. Washington, vol. 7, p. 96, pl. 2, fig. 15, ♀; 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 172. Worley, 1932, Publ. Univ. Washington Biol., vol. 1, p. 24. Roewer, 1942, Katalog der Araneae, vol. 1, p. 399. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 1255.

Types. Types of *Theridion stictum* from "roots of heath near Winchester, and at Bloxworth, Dorset," England. Two male syntypes of *Crustulina borealis* and four female syntypes of *Crustulina pallipes* from Olympia, Washington, in the Museum of Comparative Zoology.

Description. Carapace, sternum, brown; legs lighter brown. Abdomen (Fig. 3) colored as in *Steatoda borealis* or lacking a pattern; sometimes white or dark brown. Epigynum illustrated by Figure 2, male palpus by Figure 7. The openings of the epigynum of a Wisconsin specimen are not connected by a fold. Total length of females 2.2-2.7 mm. A female from Utah measured: total length, 2.6 mm. Carapace 1.06 mm. long, 1.04 mm. wide. First femur, 1.14 mm.; patella and tibia, 1.17 mm.; metatarsus 0.71 mm.; tarsus, 0.57 mm. Second patella and tibia, 0.91 mm.; third, 0.78 mm.; fourth, 1.01 mm. Total length of males 1.9-2.7 mm. A male from Utah measured: total length, 2.2 mm. Carapace 1.10 mm. long, 0.92 mm. wide. First femur, 1.04 mm.; patella and tibia, 1.10 mm.; metatarsus, 0.66 mm.;

tarsus 0.51 mm. Second patella and tibia, 0.88 mm.; third, 0.66 mm.; fourth, 0.93 mm.

Natural History. This species has been collected from leaf litter and from under boards and stones, often in moist places (Kaston, 1948; Locket and Millidge, 1953). Roth has collected it in fir needles in Oregon.

Distribution. England and parts of France (Simon, 1881; Locket and Millidge, 1953), United States to Alaska (Map 1). Judging by its wide distribution, this species is probably native to North America.

Records. Alaska: (Chamberlin and Ivie, 1947). *Newfoundland:* (Hackman, 1954). *Nova Scotia:* Annapolis Co.; Kings Co. *Quebec:* Gaspé Pen.; Brion Isl.; Niapisca Isl. *Ontario:* 36 mi. N. of North Bay; Ottawa. *Manitoba:* Riding Mtn. *British Columbia:* (Emerton, 1920); Departure Bay; Vanderhoof; Wellington. *Maine:* Aroostook Co.; Cumberland Co.; Mt. Desert Isl.; *New Hampshire:* Carroll Co.; Mt. Washington. *Massachusetts:* (Emerton, 1930); Essex Co.; Middlesex Co.; Plymouth Co. *Connecticut:* (Kaston, 1948). *New York:* (Crosby and Bishop, 1928); Rochester; Suffolk Co. *New Jersey:* Bergen Co. *West Virginia:* Pendleton Co. *Michigan. Illinois:* (Kaston, 1955). *Minnesota:* Aitkin Co. *Nebraska:* Lancaster Co. *Texas:* Hidalgo Co.; Matagorda Co. *Wyoming:* Yellowstone Natl. Pk. *Colorado:* Fort Collins. *Idaho:* Oneida Co. *Utah:* Salt Lake City; Uintah Co. *Arizona:* Coconino Co. *Washington:* (Worley, 1932); Island Co.; Olympia; Pacific Co.; San Juan Co.; Seattle; Snohomish Co.; Yakima. *Oregon:* Benton Co.; Coos Co.; Clackamas Co.; Columbia Co.; Jackson Co.; Yamhill Co. *California:* Alameda Co.; Lassen Co.; Los Angeles Co.; Mendocino Co.; Placer Co.; San Francisco; Santa Barbara; Yolo Co. *Baja California:* Islas Coronado; "San José."

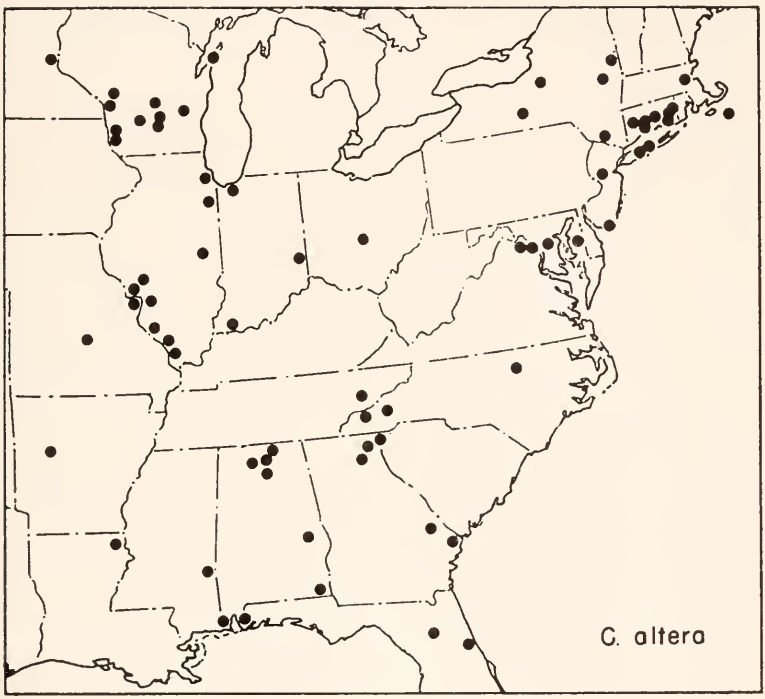
Crustulina altera Gertsch and Archer

Figures 4-6, 8-10; Map 2.

Steatoda guttata, Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 20, pl. 4, fig. 2, ♂. Emerton, 1902, The common spiders, p. 120, figs. 280-281, ♀. Not *Crustulina guttata* (Wider).

Crustulina sticta, Keyserling, 1886, Die Spinnen Amerikas, vol. 2, pt. 2, p. 37, pl. 12, fig. 154, ♀, ♂. Not *Crustulina sticta* (O.P. Cambridge).

Crustulina guttata, Banks, 1896, Jour. New York Ent. Soc., vol. 4, p. 191; 1900, Proc. Acad. Nat. Sci. Philadelphia, p. 533. Banks, 1910, Bull. U.S. Natl. Mus. no. 72, p. 21; 1911, Proc. Acad. Nat. Sci. Philadelphia, vol. 63, p. 445. Comstock, 1912, The spider book, p. 360. Barrows, 1918, Ohio Jour. Sci., vol. 18, p. 303. Emerton, 1919, Ent. News, vol. 30, p. 167. Bishop and Crosby, 1926, Jour. Elisha Mitchell Sci. Soc., vol. 41, p. 176. Crosby and Bishop, 1928, Mem. Cornell Agr. Exp. Sta.,



Map 2. Distribution of *Crustulina altera* Gertsch and Archer.

no. 101, p. 1039. Emerton, 1930, Publ. Nantucket Maria Mitchell Assoc., vol. 3, p. 164. Crosby and Bishop, 1936, Jour. New York Ent. Soc., vol. 44, p. 44. Kaston, 1938, Bull. Connecticut Geol. Nat. Hist. Surv., no. 60, p. 185. Comstock, 1940, The spider book, rev. ed., p. 375. Lowrie, 1948, Ecology, vol. 29, p. 336. Dowdy, 1950, Amer. Midland Nat., vol. 43, p. 667. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 1256, in part. Not *Crustulina guttata* (Wider).

Crustulina altera Gertsch and Archer, 1942, Amer. Mus. Novitates, no. 1171,

p. 1, fig. 9, ♀. Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 39. Muma, 1945, Bull. Univ. Maryland Agr. Exp. Sta., no. A38, p. 25. Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 20. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 74, figs. 30-33, 2119, ♀, ♂. Kaston, 1953, How to know the spiders, p. 161, fig. 403, ♀. Levi and Field, 1954, Amer. Midland Nat., vol. 51, p. 442. Kaston, 1955, Trans. Illinois Acad. Sci., vol. 47, p. 166.

Types. Male holotype and female allotype of *C. altera* from Norwalk, Connecticut, in the American Museum of Natural History.

Description. Carapace, sternum orange-brown; legs yellowish. Abdomen (Fig. 10) with brown maculations sometimes similar to that of *C. sticta.* Epigynum illustrated by Figure 5, male palpus by Figure 8. Total length of females 1.5-2.0 mm. A female from Illinois measured: total length 1.8 mm. Carapace 0.42 mm. long, 0.80 mm. wide. First patella and tibia 0.85 mm.; second, 0.67 mm.; third, 0.49 mm. Fourth femur, 0.85 mm.; patella and tibia, 0.89 mm.; metatarsus, 0.45 mm.; tarsus, 0.41 mm. Total length of males 2.0-2.3 mm. A male from Illinois measured: total length 2.3 mm.; carapace 1.23 mm. long, 0.98 mm. wide. First femur 1.07 mm.; patella and tibia, 1.18 mm.; metatarsus, 0.72 mm.; tarsus, 0.57 mm. Second patella and tibia, 0.98 mm.; third, 0.75 mm.; fourth, 1.03 mm.

Natural History. This species is found under logs and stones. In Wisconsin it is commonly collected by sifting leaf litter from relatively dry forests. In Connecticut males overwinter as adults. Egg sacs are 3 mm. in diameter made of few white threads and containing about five pink eggs (Kaston, 1948). Both Emerton (1919) and Crosby and Bishop (1939) collected it with ballooning spiders.

Distribution. Eastern United States (Map 2). There are many records from the West and Canada; however these seem to be *C. sticta.*

Records. Massachusetts: (Emerton, 1930); Boston. *Connecticut:* (Kaston, 1948). *New York:* (Crosby and Bishop, 1928; Gertsch, 1942). *New Jersey:* Cape May; Mercer Co. *Maryland:* (Muma, 1945). *District of Columbia:* Washington. *Virginia:* Fairfax Co. *North Carolina:* Durham; Buncombe Co.; Haywood Co. *South Carolina:* Stumphouse Mtn. *Georgia:* (Chamberlin and Ivie, 1944). *Florida:* (Gertsch, 1942); Volusia Co.

Alabama: (Gertsch, 1942; Archer, 1946). *Mississippi:* Lauderdale Co. *Louisiana:* (Crosby and Bishop, 1936). *Ohio:* (Barrows, 1918). *Indiana:* (Lowrie, 1948) Vanderburgh Co. *Tennessee:* (Gertsch, 1942). *Wisconsin:* (Levi and Field, 1954); Crawford Co.; La Crosse Co.; Jackson Co.; Sauk Co.; Waushara Co. *Illinois:* Bond Co.; Jackson Co.; Macoupin Co.; Piatt Co.; Union Co.; Will Co. *Minnesota:* Minneapolis. *Missouri:* (Dowdy, 1950); St. Louis. *Arkansas:* Yell Co.: Roaring River State Pk.

Steatoda Sundevall

Steatoda Sundevall, 1833, Conspectus Arachnidum, p. 16. Type species: "*Theridion 4-punctatum*" (= *Steatoda bipunctata* Linnaeus).

Asagena Sundevall, 1833, *op. cit.*, p. 19. Type species: *Asagena phalerata* Panzer.

Lithyphantes Thorell, 1869, On European spiders, p. 94. Type species: *Lithyphantes corollatus* Linnaeus (= *Steatoda albomaculata* De Geer).

Teutana Simon, 1881, Les Arachnides de France, vol. 5, p. 161. Type species: *Teutana triangulosa* Walckenaer.

Stearodea F.O.P. Cambridge, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 9, p. 193. Type species: *Aranea bipunctata* Linnaeus.

Remarks on nomenclature. Sundevall listed four species as belonging to *Steatoda,* but did not indicate the type. C.L. Koch in 1845, according to F.O.P. Cambridge, 1902, withdrew *Aranea 4-punctatum,* the first species listed, from *Steatoda* and placed it in *Eucharia.* Cambridge believed that one of the remaining species, *Theridion lunatum* ought to be the type. If we were to follow Cambridge, *Achaea* Keyserling (= *Achaearanea* Strand) would be a subjective synonym of *Steatoda.* However, it seems best to continue the usage of the last fifty years and assume *Aranea bipunctata* to be the type.

Description. Medium sized to large theridiid spiders (2-11 mm. total length). Carapace slightly longer than wide in larger species, longer than wide in smaller ones, sometimes with a circular or transverse depression. Anterior eye row straight to procurved when viewed from in front, posterior row straight or slightly recurved when viewed from above. Size of eyes variable. Carapace highest at posterior eye row. Chelicerae about as long as height of carapace with one tooth on anterior margin (Figs. 63, 87), or two (*S. moesta*). Legs of medium

length. First or fourth longest sometimes subequal in length, third shortest. A distinct comb present on fourth tarsus. Abdomen subglobular in larger species, longer than wide or high in smaller species. Colulus large (Figs. 62, 86).

Sexual dimorphism. Male slightly smaller than female. Carapace and sternum of males sometimes more rugose; carapace of male with a stridulating organ on each side of pedicel. Anterior end of abdomen above pedicel with a semicircular sclerotized carina which apparently rubs against stridulating organ. Males of many species with chelicerae enlarged, and endites swollen, sometimes with tubercles on endites. The males of some species (*S. americana*) may have the first pair of legs thicker, and the second with a spine. Males are much less common in collections than females.

Genitalia. Epigynum often with a flat plate and a median lobe projecting posteriorly. Two seminal receptacles present. Ducts heavily sclerotized in the *S. bipunctata* group. Palpus with a large radix (R in Figs. 60, 61, 69, 75, 153, 154), median apophysis (M), conductor (C) and embolus (E). Embolus may have an elaborate base which may be of diagnostic value in both the *S. fulva* and *S. bipunctata* group. Paracymbial hook (P) on the mesal side of alveolus in some species (Fig. 60) in others distal or ectal apparently holding median apophysis in all species. In *S. albomaculata* which has the paracymbial hook ectal, the median apophysis has a process which probably fits against this structure (Fig. 61).

Diagnosis. This genus differs from other theridiid genera by having a large colulus; one or two teeth on the anterior margin of the chelicerae, no teeth on the posterior. It differs from *Latrodectus* in that the lateral eyes are touching each other or are separated by less than their diameter; from *Crustulina* in lacking a spur on the mesal side of the cymbium of male palpus and lacking a sclerotized ring on the abdomen of females around the pedicel.

Distribution. Members of this genus are found in all parts of the world. Several are cosmopolitan.

Misplaced species. The following North American species described as *Lithyphantes* or *Steatoda* are misplaced.

Lithyphantes cyaneus Worley, 1928, Ann. Ent. Soc. Amer., vol. 21, p. 621, figs. 5,6, ♀, is a *Singa* (Argiopidae).

Lithyphantes mimoides Chamberlin, 1919, Jour. Ent. Zoo., vol. 12, p. 8, pl. 3, fig. 4, ♀, is *Enoplognatha marmorata* (Hentz).

Lithyphantes oophorus Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., vol. 30, p. 170, figs. 8, 9, ♀, is *Coleosoma floridana* Banks.

Steatoda fusca Emerton, 1894, Trans. Connecticut Acad. Sci., vol. 9, p. 407, pl. 2, fig. 1, ♀, ♂ is a *Ctenium*.

Steatoda nigra Emerton, 1884, Trans. Connecticut Acad. Sci., vol. 6, p. 21, pl. 4, fig. 4, ♀, ♂ is a *Dipoena*.

F.O.P. Cambridge (1902, Biologia Centrali Americana, Araneidea, vol. 2) described several species of *Theridion* in the genus *Steatoda*.

STEATODA NIGROFEMORATA (Keyserling), new combination

Figures 11-13; Map 3.

Lithyphantes nigrofemoratus Keyserling, 1882, Die Spinnen Amerikas, vol. 2, no. 1, p. 139, pl. 6, fig. 87, ♀. F.O.P. Cambridge, 1902, Biologia Centrali Americana, Araneidea, vol. 2, p. 376, pl. 35, fig. 14, ♀. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183. Chamberlin, 1916, Bull. Mus. Comp. Zool., vol. 60, p. 232. Banks, 1929, *ibid.*, vol. 69, p. 86. Mello-Leitão, 1941, Rev. Mus. La Plata, vol. 2, p. 141. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408.

Asagena alticeps Keyserling, 1886, Die Spinnen Amerikas, vol. 2, pt. 2, p. 4, fig. 136, ♂. Simon, 1894, Histoire naturelle des Araignées, vol. 1, p. 576. F.O.P. Cambridge, 1902, Biologia Centrali Americana. Araneidea, vol. 2, p. 377, pl. 35, fig. 16, ♂. Simon, 1903, Histoire naturelle des Araignées, vol. 2, p. 990. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 170. Reimoser, 1939, Ann. Naturhist. Mus. Wien, vol. 50, p. 344. Mello-Leitão, 1940, Arq. Zool., vol. 12, p. 176. Roewer, 1942, Katalog der Araneae, vol. 1, p. 396. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 752. Caporiacco, 1955, Acta Biol. Venezuelica, vol. 1, p. 329, fig. 22, ♀. NEW SYNONYMY.

Lithyphantes laetus O.P. Cambridge, 1896, Biologia Centrali Americana, Araneidea, vol. 1, p. 181, pl. 22, fig. 12, ♂. NEW SYNONYMY.

?*Asagena patagonica* Tullgren, 1901, Svenska Exped. Magellansländerna, vol. 2, no. 10, p. 194, pl. 15, fig. 4, ♀. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 171. Roewer, 1942, Katalog der Araneae, vol. 1, p. 397. NEW SYNONYMY.

Types. Female holotype of *Lithyphantes nigrofemoratus* from Monte Rico. Peru, in the collection of the University of War-

saw, Poland. Male holotype of *Asagena alticeps* from Nueva Granada, Colombia. Male holotype of *Lithyphantes laetus* from Costa Rica in the British Museum (Natural History). Three female syntypes of *Asagena patagonica* from Patagonia, probably in the Riksmuseum, Stockholm.

Description. Carapace, sternum, legs yellow-brown; femora much darker, ends of tibiae darker. Abdomen black, dorsum usually with two transverse lines, an anterior one and one posterior which is broken on each side. South American specimens often with spots on dorsum; venter with a white spot behind genital groove. Anterior median eyes smaller than

Map 3. Distribution of *Steatoda nigrofemorata* (Keyserling).

others, one diameter apart, one-half to one diameter from laterals. Posterior median eyes three-quarters their diameter apart, a little more than one diameter from laterals. Male chelicerae enlarged, lacking distinct tooth on anterior margin. Epigynum with a wrinkled scape (Fig. 13), male palpus illustrated by Figure 11. The embolus of the palpus is sometimes broken off. Total length of females 3.8-4.3 mm. A female from Panama measured: total length, 4.2 mm. Carapace 1.6 mm. long, 1.2 mm.

wide. First patella and tibia, 1.7 mm.; second, 1.5 mm.; third, 1.3 mm. Fourth femur, 1.5 mm.; patella and tibia, 1.8 mm.; metatarsus, 1.1 mm.; tarsus, 0.7 mm. Total length of males 3.3-3.5 mm. A male from Panama measured total length, 3.5 mm. Carapace 1.8 mm. long, 1.1 mm. wide. First patella and tibia, 1.6 mm.; second, 1.5 mm.; third, 1.2 mm. Fourth femur, 1.6 mm.; patella and tibia, 1.9 mm.; metatarsus, 1.3 mm.; tarsus, 0.7 mm. Tullgren's specimens were larger, total length 6 mm.

Natural History. This species has been collected under a fallen tree in Peru. Tullgren found his in dry, sandy localities.

Distribution. South America, north to Veracruz (Map 3).

Records. Veracruz: 10 mi. S. of San José del Carmen. *Guatemala:* Quiriguá. *Nicaragua:* Musawas, Waspuc River. *Costa Rica:* (Reimoser, 1939). *Panama:* Barro Colorado Island; Boquete; La Compana; Santa Rosa, Colon Prov. *Venezuela:* (Caporiacco, 1955). *British Guiana:* (Mello-Leitão, 1940). *Peru:* (Chamberlin, 1916); Ayacucho; Húanuco; Huancayo; Tingo María; Pucará. *Brazil:* Minas Geraes; Minha Serinha Diamantina. Parana: Cavinna; Rolândia. *Argentina:* (Tullgren, 1901; Mello-Leitão, 1941); Salta.

Steatoda moesta (O.P. Cambridge), new combination

Figures 15-18; Map 4.

Steatoda brasiliana, Keyserling, 1886, Die Spinnen Amerikas, vol. 2, pt. 2, p. 238, pl. 20, fig. 293,♀. Not *Steatoda brasiliana* Keyserling, 1884, *ibid.,* pt. 1, p. 115, pl. 5, fig. 75,♂.

Asagena moesta O.P. Cambridge, 1896, Biologia Centrali Americana, Araneidea, vol. 1, p. 209, pl. 25, fig. 4,♀. F.O.P. Cambridge, 1902, *ibid.,* vol. 2, p. 35, fig. 18,♀. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 170. Roewer, 1942, Katalog der Araneae, vol. 1, p. 397. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 753. Kraus, 1955, Abhandl. Senckenbergischen Naturf. Gesell., no. 493, p. 15.

Type. Female type of *Asagena moesta* from Guatemala in the British Museum (Natural History).

Description. Carapace, sternum dark brown. Legs dark brown, except fourth, which have femora and tibiae orange brown, with ends darker. Abdomen black with white marks on dorsum (Fig. 15); venter with white marks on each side of

epigastric area. Male with sclerotized portions orange brown. Eyes subequal in size. Anterior median eyes separated by two-thirds their diameter. Posterior medians two-thirds diameter apart, two-thirds to one diameter from laterals. Chelicerae with two teeth on anterior margin. Epigynum a black spot in a lighter area, posterior to which is a small scape (Fig. 17). In South American specimens the black spot may be larger, the posterior scape indistinct. Coloration and shape quite variable. Male palpus illustrated by Figure 18. Total length of females 4.8-8.7 mm. A female from Panama measured total length, 8.7 mm. Carapace 3.8 mm. long; 3.3 mm. wide. First femur, 5.0 mm.;

Map 4. Distribution of *Steatoda moesta* (O.P. Cambridge) and *S. saltensis*, new species.

patella and tibia, 5.4 mm.; metatarsus, 4.0 mm.; tarsus, 1.8 mm. Second patella and tibia, 4.3 mm.; third, 3.5 mm.; fourth, 4.9 mm. Total length of males, 6.2-8.0 mm. A male from Panama measured total length, 6.5 mm. Carapace 3.4 mm. long; 2.5 mm. wide. First femur, 4.3 mm.; patella and tibia, 4.3 mm.; metatarsus, 3.3 mm.; tarsus, 1.6 mm. Second patella and tibia, 3.6 mm.; third, 2.7 mm.; fourth, 4.2 mm.

Distribution. From Tabasco to Brazil, Map 4.

Records. Tabasco: Teapa (C. and M. Goodnight), ♀. *Chiapas:* Río Huixtla, N. of Huixtla (T. C. Schneirla), ♀. *El Salvador:* (Kraus, 1955). *Panama:* El Valle (A. M. Chickering), ♀, ♂:

Barro Colorado Island (A. M. Chickering), ♀, ♂. *Peru:* Dept. Huanuco; Acomayo, 2160 m. (F. Woytkowski), ♀. *Brazil:* Est. Rio de Janeiro: Teresopolis (H. Sick), ♀.

Steatoda quaesita (O.P. Cambridge), new combination

Figure 14.

Lithyphantes quaesitus O.P. Cambridge, 1896, Biologia Centrali Americana, Araneidea, vol. 1, p. 180, pl. 22, fig. 6, ♂. F.O.P. Cambridge, 1902, *ibid.*, vol. 2, p. 376, pl. 35, fig. 13, ♂. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408.

Type. Male holotype from Teapa, Tabasco, in the British Museum (Natural History).

Only the palp of the type was examined. It is probably the male of either *S. saltensis* or more likely that of *S. autumnalis.*

Steatoda saltensis, new species

Figures 19, 20; Map 4.

Lithyphantes lugubris F.O.P. Cambridge, 1902, Biologia Centrali Americana, Araneidea, vol. 2, p. 376 (in part), pl. 35, fig. 15c (not fig. 15b).

Types. Female holotype and one female paratype from forty miles northeast of El Salto, Durango, Mexico, Aug. 11, 1947 (W. J. Gertsch), in the American Museum of Natural History.

Description. Carapace, sternum, legs brown. Abdomen black with a light transverse anterior band; venter with a white line behind genital furrow. Eyes subequal in size. Anterior median eyes one diameter apart, three-quarters of a diameter from laterals. Posterior median eyes one diameter apart, one and three-quarters diameters from laterals. Laterals separated by three-quarters diameter. Total length of females 7.6-10.3 mm. The holotype measured total length 10.3 mm. Carapace 3.7 mm. long; 3.0 mm. wide. First femur, 4.3 mm.; patella and tibia, 4.8 mm.; metatarsus, 3.7 mm.; tarsus, 1.4 mm. Second patella and tibia, 4.0 mm.; third, 3.0 mm.; fourth, 4.7 mm.

Diagnosis. Only details of the epigynum (Fig. 20) distinguish this species from the related *Steatoda autumnalis.*

Distribution. Central Mexico (Map 4). A female paratype of *L. lugubris* which F.O.P. Cambridge thought to be immature

was collected in Bugaba, Panama. Recent Panamanian collectors have not included *S. saltensis* again.

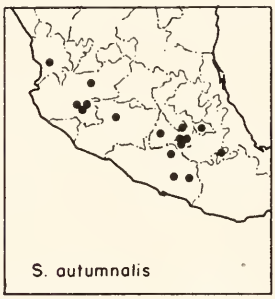
Records. Durango: 30 mi. NE. of El Salto, Aug. 11, 1947 (W. J. Gertsch), ♀. *Distrito Federal:* Contreras, May 30, 1946, 8000-9000 ft. (J.C. and D.L. Pallister), ♀. *?Zacatecas:* Tenayuca, July 14, 1943 (C. Bolivar), ♀.

Steatoda autumnalis (Banks), new combination

Figures 21, 22; Map 5.

Lithyphantes autumnalis Banks, 1898, Proc. California Acad. Sci., 3rd. ser., vol. 1, p. 240, pl. 14, fig. 6. F.O.P. Cambridge, 1902, Biologia Centrali Americana, Araneidea, vol. 2, p. 376. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 182. Roewer, 1942, Katalog der Araneae vol. 1, p. 407.

Lithyphantes clarus O.P. Cambridge, 1898, Biologia Centrali Americana, Araneidea, vol. 1, p. 252, pl. 38, fig. 6. F.O.P. Cambridge, 1902, *ibid.*, vol. 2, p. 376. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 182. Roewer, 1942, Katalog der Araneae, vol. 1, p. 407. NEW SYNONYMY.



Map 5. Distribution of *Steatoda autumnalis* (Banks).

Lithyphantes lugubris F.O.P. Cambridge, 1902, Biologia Centrali Americana, Araneidea, vol. 2, p. 376, (in part), pl. 35, fig. 15b (not 15c). Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183. ? Banks, 1913, Proc. Acad. Nat. Sci. Philadelphia, p. 678. ? Reimoser, 1937, Ann. Naturhist. Mus. Wien, vol. 50, p. 344. Roewer, 1942. Katalog der Araneae, vol. 1, p. 408. NEW SYNONYMY.

Types. Immature, less than half grown, holotype of *Lithyphantes autumnalis* Banks, from Tepic, Nayarit, in the Museum

of Comparative Zoology. Immature holotype of *Lithyphantes clarus* from Pátzcuara, Michoacan. Female holotype of *Lithyphantes lugubris* from Omiltemi, Guerrero. The last two are in the British Museum (Natural History).

Remarks on nomenclature. Although the types of *Lithyphantes autumnalis* and *L. clarus* can not be determined with absolute certainty, *L. autumnalis* has the typical pattern of the juvenile of this species, and adults have been collected in the type locality. *L. clarus* is probably a penultimate female, judging by its coloration. The type locality is well within the range of this species. The publication date of *L. autumnalis* is May 28, 1898; that of *L. clarus,* June, 1898.

Description. Carapace, sternum, legs dark brown. Abdomen black with a white stripe around anterior margin of dorsum; venter with a short white transverse line behind genital groove. Immatures seem to have abdomen brightly colored with patches of light and dark pigment. Eyes on slight tubercles; anterior medians slightly smaller than others, one diameter apart, and one diameter from laterals. Posterior median eyes one diameter apart, one and one-half diameters from laterals. Epigynum illustrated by Figure 22. Total length of females 7.8-11.0 mm. A female measured: total length 8.7 mm. Carapace 3.7 mm. long, 3.0 mm. wide. First femur, 4.0 mm.; patella and tibia, 4.9 mm.; metatarsus, 3.5 mm.; tarsus, 1.3 mm. Second patella and tibia, 3.3 mm.; third, 3.0 mm.; fourth, 4.4 mm. The male is not known.

Distribution. Central Mexico. Map 5. The records of Costa Rica and Panama (F.O.P. Cambridge, 1902; Banks, 1913; Reimoser, 1939) are probably erroneous.

Records. Nayarit: Tepic. *Jalisco:* Nevado de Colima; Tlaquepague; W. side of Lake Sayula; Tizapán. *Mexico:* Ixtapan de la Sal. *Distrito Federal:* Santa Rosa. *Morelos:* Oaxtepec; Acatlipa; Cuantla. *Tlaxcala:* Tlaxcala. *Puebla:* Tehuacan. *Guerrero:* Taxco; 23 mi. S. of Chilpancingo.

Steatoda transversa (Banks), new combination

Figures 23-27; Map 6.

Lithyphantes transversus Banks, 1898, Proc. California Acad. Sci., 3rd ser., vol. 1, p. 240, pl. 14, fig. 5, ♀. Petrunkevitch, 1911, Bull. Amer. Mus.

Nat. Hist., vol. 29, p. 183. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408.

Type. One female from El Taste, Baja California, in the Museum of Comparative Zoology.

Description. Carapace, sternum, legs, orange-brown. Abdomen dark purplish with white spots on dorsum and indistinct white spots on venter. Anterior lateral eyes largest, posterior laterals slightly smaller, median eyes subequal and smallest. Anterior medians three-quarters diameter apart, the same distance from laterals. Posterior medians half their diameter apart, one diameter from laterals. Chelicerae of male slightly swollen and endites enlarged. Epigynum (Fig. 24) with two dark spots

Map 6. Distribution of *Steatoda transversa* (Banks).

slightly more than their diameter apart. Male palpus illustrated by Figures 26, 27. A female from Arizona measured: total length, 4.3 mm. Carapace 1.6 mm. long, 1.3 mm. wide. First patella and tibia, 1.4 mm.; second, 1.2 mm.; third, 1.0 mm. Fourth femur, 1.3 mm.; patella and tibia, 1.7 mm.; metatarsus, 0.9 mm.; tarsus, 0.7 mm. A male from Arizona measured: total length, 3.1 mm. Carapace 1.6 mm. long, 1.1 mm. wide. First patella and tibia, 1.3 mm.; second, 1.1 mm.; third, 0.9 mm. Fourth femur, 1.2 mm.; patella and tibia, 1.4 mm.; metatarsus, 0.9 mm.; tarsus, 0.6 mm.

Natural History. Roth collected this species in Arizona by sweeping an alfalfa field.

Distribution. Texas, Arizona to Oaxaca. Map 6.

Records. Texas: Hays Co.; Hidalgo Co.: Edinburg. *Arizona:* Yuma Co.: Yuma Mesa. *California:* Riverside Co.: Indio. *Sonora:* 10 mi. S. of Hermosillo. *Nayarit:* Acaponeta; Jesús María. *Jalisco:* Plan de Barrancas. *Colima:* 20 mi. N.; 7 mi. S. of Colima; Manzanillo. *Morelos:* Alpuyecca. *Veracruz:* Plan del Río. *Oaxaca:* Oaxaca.

Steatoda quadrimaculata (O.P. Cambridge), new combination

Figures 28-31; Map 7.

Asagena quadrimaculata O.P. Cambridge, 1896, Biologia Centrali Americana, Araneidea, vol. I, p. 189, pl. 23, fig. 12, ♂. Simon, 1897, Proc. Zool. Soc. London, p. 864. F.O.P. Cambridge, 1902, Biologia Centrali Americana, Araneidea, vol. 2, p. 378, pl. 35, fig. 17, ♂. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 171. Chickering, 1936, Trans. Amer. Micros. Soc., vol. 55, p. 451. Bryant, 1940, Bull. Mus. Comp. Zool., vol. 86, p. 302. Roewer, 1942, Katalog der Araneae, vol. 1, p. 397. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 757.

Lithyphantes hermosa Banks, 1909, Proc. Acad. Nat. Sci. Philadelphia, vol. 61, p. 205, pl. 6, fig. 44, ♀. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 182. Reimoser, 1939, Ann. Naturhist. Mus. Wien, vol. 50, p. 344. Roewer, 1942, Katalog der Araneae, vol. 1, p. 407. NEW SYNONYMY.

Lithyphantes tricolor Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 44, figs. 67-74, ♀. NEW SYNONYMY.

Asagena marcuzzii Caporiacco, 1955, Acta Biol. Venezuelica, vol. 1, p. 330, fig. 23, ♀. NEW SYNONYMY.

Types. Male holotype of *Asagena quadrimaculata* from Antigua, Guatemala, in the British Museum (Natural History). Female holotype of *Lithyphantes hermosa* from Punta Arenas, Costa Rica, in the Museum of Comparative Zoology. Female holotype of *Lithyphantes tricolor* from Savannah Beach, Georgia, in the American Museum of Natural History. Female holotype of *Asagena marcuzzii* from Maiquetía, D.F., Venezuela, in the Museo de Biologia, Universidad Central di Venezuela.

Description. Carapace, sternum, legs yellow to orange, some

duskiness on femora. Abdomen dark purple with 6 or 7 dorsal white spots, a U-shaped light spot on venter and smaller spots on each side. Anterior median eyes slightly smaller than others, separated by three-quarters diameter, one-third diameter from laterals. Posterior medians separated by one-third diameter, one-half to one diameter from laterals. Lateral eyes not separated. Chelicerae and endites of males enlarged. Epigynum with a dark spot each in a pair of depressions (Fig. 29). Male palpus illustrated by Figures 30, 31. Total length of females 2.7-4.0 mm. A female from Tamaulipas measured total length, 3.6 mm. Carapace 1.36 mm. long, 0.98 mm. wide. First patella and tibia, 1.35 mm.; second, 1.13 mm.; third, 0.95 mm. Fourth femur, 1.17 mm., patella and tibia, 1.42 mm.; metatarsus, 0.78; tarsus, 0.52 mm. Total length of males, 2.2-3.2 mm. A male from

Map 7. Distribution of *Steatoda quadrimaculata* (O.P. Cambridge).

Tamaulipas measured: total length, 3.1 mm. Carapace 1.60 mm. long, 1.14 mm. wide. First patella and tibia, 1.54 mm.; second, 1.36 mm.; third, 1.10 mm. Fourth femur, 1.40 mm.; patella and tibia, 1.74 mm.; metatarsus, 1.20 mm.; tarsus, 0.60 mm.

Distribution. Southern United States to northern South America. Map 7.

Records. Florida: Alachua Co.; Collier Co.; Highlands Co. *Alabama:* Baldwin Co. *Mississippi:* Covington Co. *Louisiana:* Beauregard Par.; St. Helena Par.; Shreveport. *Texas:* Chambers

Co., Hidalgo Co.; Starr Co. *Tamaulipas:* 20 mi. N. of Lemon; 2 mi. E. of Nuevo Morelos; 13-15 mi. S., 27 mi. N., 35 mi. N. of Villa Juárez. *San Luis Potosí:* Tamazunchale; 2 mi. N. of Tamazunchale; 5 mi. N., 10 mi. N., 13 mi. N. of Valles; Valles. *Hidalgo:* Chapulhuacán. *Veracruz:* Córdoba. *Nayarit:* Campostela; La Libertad. *Colima:* 25 mi. E. of Mazamitla. *Guerrero:* Lo Bajo; Arcelia; 32 mi. N. of Acapulco. *Oaxaca:* Palomares; Soledad; Tolosa; San Felipe; Tehuantepec. *Chiapas:* Las Cruzes. *Is. Revillagigedo:* Socorro Is. *Panama:* (Chickering, 1936). *Cuba:* (Bryant, 1940). *Lesser Antilles:* (Simon, 1897). *Venezuela:* (Simon, 1897).

Steatoda fulva group

This group is represented by three similar species which are sympatric over most of their ranges.

Description. Carapace, sternum, legs orange to brown; sometimes legs red-brown with distal segments lighter. Abdomen purplish brown with dorsal white spots (Figs. 51, 52, 54, 55), venter with a white spot posterior to the genital groove, another anterior to spinnerets, both frequently connected by a white line. *S. pulcher* may be differently colored. In all three species eyes subequal in size; or frequently anterior medians larger than others, rarely slightly smaller. Anterior medians one-half to one diameter apart, one-quarter to one-half their diameter from laterals. Posterior eyes equi-distant, two-thirds to one diameter apart. Lateral eyes slightly separated or touching each other. The genitalia and measurements are similar.

Variation. The coloration is variable in *S. medialis* and *S. pulcher.* The epigyna of all three species, the palp of *S. medialis* and *S. pulcher* are variable.

Natural History. Virtually nothing is known of the natural history of these three species. It is assumed that all three are found in arid situations under stones, logs and in debris.

Key to females of the Steatoda fulva *group*

1. Anterior edge of "transverse bridge" of epigynum pointing anterior; "bridge" semicircular in cross-section (Figs. 43, 44) ..... *medialis*

1. Anterior edge of "bridge" of epigynum, straight or pointing posterior. (Figs. 46, 49) 2
2. Posterior edge of "bridge" with two lobes each as wide as intermediate area, bridge flat in cross-section. (Fig. 49, 50) ...*pulcher*
2. Posterior edge of "bridge" more or less straight with lobes widely separated. (Figs. 46, 47) ....*fulva*

Key to males of the STEATODA FULVA *group*

1. Palpus in ventral view with large portion of median apophysis showing on mesal side, outside embolic tube (Figs. 34-36) .....*medialis*
1. Palpus in ventral view with only edge of median apophysis showing on mesal side outside of embolic tube (Figs. 32, 38, 41) 2
2. Palpus in ventral view with area surrounded by embolic tube as high as wide, subcircular; basal membrane of embolus covering less than one half of area enclosed by embolus (Figs. 32, 33) .....*fulva*
2. Palpus in ventral view with area surrounded by embolic tube elliptical, much wider than high (Figs. 39, 41); *or* with area surrounded by embolic tube subcircular with basal membrane of embolus covering more than half of enclosed area (Fig. 38) .....*pulcher*

STEATODA MEDIALIS (Banks), new combination

Figures 34-36, 42-44, 53-55; Map 8.

Steatoda distincta Thorell, 1877, Bull. U.S. Geol. Surv., vol. 3, p. 485. Banks, 1893, Jour. New York Ent. Soc., vol. 1, p. 124; ? 1895, Ann. New York Acad. Sci., vol. 8, p. 423; 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 188. Not *Steatoda distincta* (Blackwall).

Lithyphantes punctulata Marx, 1898, in Banks, Proc. California Acad. Sci., 3rd ser., vol. 1, p. 239, pl. 14, fig. 4, ♀. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408. NEW SYNONYMY.

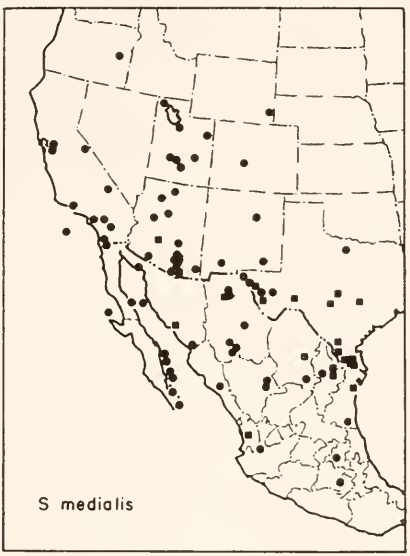
Lithyphantes medialis Banks, 1898, Proc. California Acad. Sci., 3rd. ser., vol. 1, p. 240, pl. 14, fig. 3, ♀. Banks, 1902, Proc. U.S. Natl. Mus., vol. 25, p. 214. Banks, 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183.

Lithyphantes distincta, Chamberlin, 1933, Bull. Univ. Utah, biol. ser., vol. 2, no. 2, p. 8, pl. 1, fig. 9, ♀. Gertsch, 1935, Amer. Mus. Novitates, no. 792, p. 21. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408.

Types. Female type of *Steatoda distincta* from Colorado in the Riksmuseum, Stockholm. One female syntype and fragments of two juveniles of *Lithyphantes punctulata* are alleged to have come from Las Palmas, Baja California, in the Museum of Comparative Zoology. Two female syntypes of *Lithyphantes medialis*

from San José del Cabo, Baja California, in the Museum of Comparative Zoology.

Remarks on nomenclature. The name *Steatoda distincta* Thorell is not available since *Latrodectus distincta* Blackwall, 1859 (Ann. Mag. Nat. Hist., ser. 3, vol. 4, p. 260) probably belongs to this genus and had been placed by Roewer (1942) in *Lithyphantes.* Although *Lithyphantes punctulata* has page priority over *L. medialis*, Banks' name *medialis* is here used. I doubt that the type specimens of *L. punctulata* came from Baja California as indicated; they appear to come from the eastern



Map 8. Distribution of *Steatoda medialis* (Banks). Squares: many spotted coloration; circles: few spotted coloration.

portion of its range. As the type locality is uncertain, the name *L. medialis* seems preferable.

Description. Epigynum illustrated by Figures 43, 44; male palpus by Figures 34-36. Total length of females 3.2-6.5 mm. A female from California measured: total length 5.6 mm. Carapace 2.1 mm. long, 1.7 mm. wide. First femur, 2.7 mm.; patella and tibia, 2.9 mm.; metatarsus, 2.3 mm.; tarsus, 0.9 mm. Second

patella and tibia, 2.3 mm.; third, 1.9 mm.; fourth, 2.9 mm. Total length of males 2.9-5.8 mm. A male from California measured: total length 5.4 mm. Carapace 2.4 mm. long, 1.6 mm. wide. First femur, 3.0, mm.; patella and tibia, 3.4 mm.; metatarsus, 2.7 mm.; tarsus, 1.2 mm.; Second patella and tibia, 2.9 mm.; third, 2.4 mm.; fourth, 3.4 mm.

Variation. There is considerable individual variation in the shape of the epigynum, and relative eye size. The palpal tibia is long in western specimens (Fig. 36), short in eastern ones (Fig. 34).

The difference in dorsal marking is striking. Eastern specimens commonly have four rows of spots on the dorsum of abdomen (Fig. 55), western ones have only one row of large spots with one spot on each side (Fig. 54). Specimens from the center of the range from Utah to central Mexico often lack spots. A number of specimens from the Gulf of California had three lines of spots. The type of *L. punctulata* is of the variety with four rows of spots, *L. medialis* of the variety with one row. Map 8 shows the variety having four rows of spots as squares, the fewer-spotted, or those lacking spots, by circles. Collections having both patterns or the few individuals of intermediate pattern are also indicated by circles.

Natural History. This species has been collected in Colorado under stones in an arid area at 7000 feet elevation.

Distribution. Wyoming, Utah to Hidalgo. Map 8.

Records. Texas: Austin; El Paso; Hidalgo Co.; Hudspeth Co.; Jeff Davis Co.; Kerr Co.; Llano Co.; Presidio Co.; Starr Co.; Terrell Co.; Webb Co.; Wise Co.; Zapata Co. *Wyoming:* Hawk Springs, Goshen Co. Aug. 5, 1952 (B. Malkin). *Colorado:* Chaffee Co. *New Mexico:* Eddy Co.; Luna Co.; San Miguel Co. *Utah:* (Chamberlin and Ivie, 1933); Emery Co.; Salt Lake City; Sevier Co.; Uintah Co.; Wayne Co. *Arizona:* (Banks, 1902; Gertsch, 1935); Cochise Co.; Coconino Co.; Gila Co.; Organ Pipe Natl. Mon.; Phoenix; Pima Co.; Santa Cruz Co.; Tucson. *Oregon:* Malheur Co.: Malheur Riv. Canyon, Sept. 10, 1949 (V. Roth). *California:* Berkeley; Contra Costa Co.; Inyo Co.; Los Angeles Co.; Mono Co.; Riverside Co.; San Bernandino Co.; San Diego Co.; San Nicolas Isl.; Santa Barbara. *Tamaulipas:* 20 mi. E. of Villa Juárez; Arroyo Chorreras. *Nuevo León:* nr. Monterey; 30 mi. E. of General Bravo; China. *Coahuila:* 5 mi.

W. of Saltillo; La Gloria. *Chihuahua:* Primavera, 5500-6000 ft.; Huejotitlán; 50 mi. S. Ahumada; 5 mi. S. Chihuahua; 6 mi. S. Gallego; La Sauceda, 7000 ft.; Valle de Olivos, 5000 ft. *Sonora:* Punta Penasco; 15 mi. W. Agiabambo; Guaymas; Navajoa; Isla Pelícano. *Baja California:* San José del Cabo; 45 mi. E. of Tecate, 3600 ft.; Isla. Cedros; Isla. Habana; Sal Si Puedes Isl.; Carman Isl.; Coronados Isl.; Smith's Isl.; La Paz; Santa Cruz Isl. *Durango:* San Juan del Río; La Loma. *Sinaloa:* 6 mi. S. Caliacán. *Nayarit. Jalisco:* 20 mi. N. of La Quemada. *Distrito Federal:* Teotihuacán. *Hidalgo:* Ixmiquilpan.

Steatoda fulva (Keyserling), new combination

Figures 32, 33, 45-47, 52; Map 9.

Lithyphantes fulvus Keyserling, 1882, Die Spinnen Amerikas, vol. 2, pt. 1, pl. 6, fig. 89,♀. Marx, 1889, Proc. U.S. Natl. Mus. vol. 12, p. 522. Banks, 1899, Proc. Ent. Soc. Washington, vol. 4, p. 189; 1900, Proc. Acad. Nat. Sci. Philadelphia vol. 52, p. 533; 1904, *ibid.*, vol. 56, p. 653; 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 182. Comstock, 1912, The spider book, p. 362, fig. 368,♀. Worley and Pickwell, 1931, Univ. Nebraska Studies, vol. 27, p. 27. Fox, 1940, Proc. Biol. Soc. Washington, vol. 53, p. 41. Comstock, 1940, The spider book, rev. ed., p. 377, fig. 368,♀. Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., vol. 6, no. 3, p. 11. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408. Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 44.

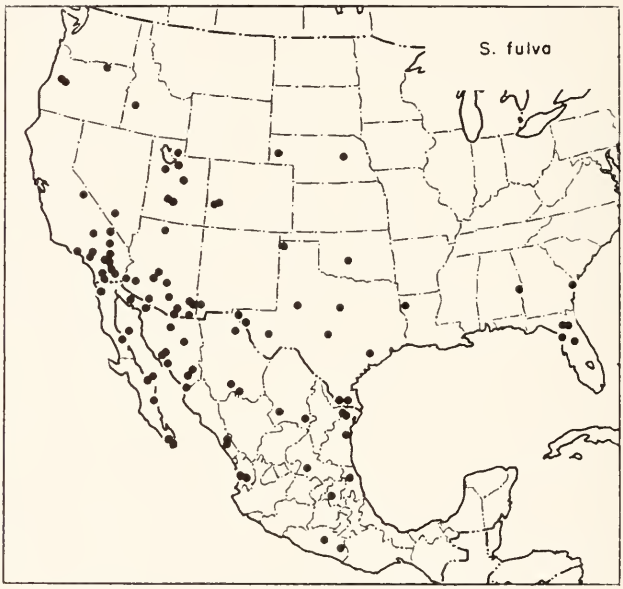
Lithyphantes parvula Banks, 1898, Proc. California Acad. Sci., 3rd. ser., vol. 1, p. 238, pl. 14, fig. 1,♀,♂. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408. NEW SYNONYMY. Not *Steatoda parvula* Saito, 1933.

Lithyphantes pulcher, Banks, 1898, Proc. California Acad. Sci., 3rd. ser., vol. 1, p. 238, pl. 14, figs. 7, 8,♀. Chamberlin, 1924, *ibid.*, 4th ser., vol. 12, p. 640. Banks et al., 1932, Publ. Univ. Oklahoma Biol. Surv., vol. 4, no. 1, p. 22. Not *Lithyphantes pulcher* Keyserling.

Lithyphantes venusta Marx, 1898, *in* Banks, Proc. California Acad. Sci., 3rd. ser. vol. 1, p. 239, pl. 14, fig. 2,♀. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183; Roewer, 1942, Katalog der Araneae, vol. 1, p. 408. NEW SYNONYMY.

Teutana nesiotes Chamberlin, 1924, Proc. California Acad. Sci., 4th ser., vol. 12, p. 639, fig. 80,♀. Roewer, 1942, Katalog der Araneae, vol. 1, p. 417. NEW SYNONYMY.

Types. Female lectotype of *Lithyphantes fulvus* from Spring Lake, Sevier County, Utah, designated by Fox, 1940, in the United States National Museum. Three male and one female syntypes of *Lithyphantes parvula* from San José del Cabo, Baja California, in the Museum of Comparative Zoology. Female type of *Lithyphantes venusta* from San Francisquito, Baja California, destroyed. Female holotype of *Teutana nesiotes* from Granite Island, north of Angel de la Guarda Island, Gulf of California, in the California Academy of Sciences; one paratype in the Museum of Comparative Zoology.



Map 9. Distribution of *Steatoda fulva* (Keyserling).

Description. Epigynum rather small and indistinct (Figs. 46, 47), male palpus illustrated by Figures 32 and 33. Total length of females, 3.0-5.9 mm. A female from California measured: total length 4.7 mm. Carapace 2.1 mm. long, 1.6 mm. wide. First patella and tibia, 2.2 mm.; second, 1.8 mm.; third, 1.5 mm. Fourth femur, 2.0 mm.; patella and tibia, 2.3 mm.; metatarsus, 1.5 mm.; tarsus, 0.8 mm. Total length of males,

2.4-5.0 mm. A male from California measured: total length 5.0 mm. Carapace 2.3 mm. long, 1.9 mm. wide. First patella and tibia, 2.8 mm.; second, 2.4 mm.; third, 2.1 mm. Fourth femur, 2.7 mm.; patella and tibia, 3.1 mm.; metatarsus, 2.3 mm.; tarsus, 0.9 mm.

Natural History. This species is probably found under stones in dry areas. It has also been collected in a house in Yuma, Arizona.

Distribution. Southern and western United States south to central Mexico. Map 9.

Records. Georgia: (Fox, 1940; Chamberlin and Ivie, 1944). *Florida:* (Banks, 1904); Alachua Co.; Lake Co.; Putnam Co. *Alabama:* (Banks, 1900). *Louisiana:* (Banks, 1899). *Nebraska:* (Worley and Pickwell, 1931); Platte Co.; Columbus, June 26, 1946 (M. H. Muma). *Oklahoma:* (Banks et al., 1932). *Texas:* (Fox, 1940); Brewster Co.; Dallam Co.; El Paso; Hidalgo Co.; Howard Co.; Hudspeth Co.; Llano Co. Somervell Co.; Starr Co. *Colorado:* Mesa Co. *New Mexico:* Hidalgo Co. *Idaho:* Boise, June 15, 1941 (B. Malkin). *Utah:* Carbon Co.; Salt Lake City; Sevier Co.; Tooele Co.; Weber Co. *Nevada:* Nye Co. *Arizona:* Cochise Co.; Coconino Co.; Maricopa Co.; Organ Pipe Cactus Natl. Mon.; Pima Co.; Pinal Co.; Santa Cruz Co.; Yuma Co. *Oregon:* Lake Co.; Umatilla. *California:* Imperial Co.; Inyo Co.; Los Angeles Co.; Mono Co.; Riverside Co.; San Bernardino Co.; San Diego Co.; Ventura Co.

Steatoda pulcher (Keyserling), new combination

Figures 37-41, 48-51; Map 10.

Lithyphantes pulcher Keyserling, 1882, Die Spinnen Amerikas, vol. 2, pt. 1, p. 137, pl. 6, fig. 85, ♀. Marx, 1898, Proc. U.S. Natl. Mus., vol. 12, p. 522. Banks, 1910, Bull. U.S. Natl. Mus., no. 72, p. 21 (in part). Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 183 (in part). Roewer, 1942, Katalog der Araneae, vol. 1, p. 408 (in part).

Type. Female holotype from Washington Territory in the Muséum d'Histoire Naturelle in Paris.

Description. Epigyna illustrated by Figures 49, 50; male palpus by Figures 37-41. Total length of females 3.0-6.8 mm. A female from Coahuila measured: total length 5.0 mm. Carapace 1.8 mm. long, 1.5 mm. wide. First femur 2.2 mm.; patella

and tibia, 2.6 mm.; metatarsus, 1.8 mm.; tarsus, 0.86 mm. Second patella and tibia 2.0 mm.; third, 1.7 mm.; fourth, 2.6 mm. Total length of males 2.8-5.8 mm. A male from Coahuila measured: total length, 3.2 mm. Carapace, 1.4 mm. long, 1.1 mm. wide. First femur, 1.7 mm.; patella and tibia, 2.1 mm.; metatarsus, 1.5 mm.; tarsus, 0.7 mm. Second patella and tibia 1.6 mm.; third, 1.2 mm.; fourth, 2.0 mm.

Variation. Some specimens have the fourth leg longer than the first, in others the first is longest. There is considerable individual variation in the shape of the epigynum (Figs. 49,

Map 10. Distribution of *Steatoda pulcher* (Keyserling).

50). All the largest specimens came from northern California and Oregon, most of the smallest from Texas; specimens from other regions are intermediate in size. The largest specimens from northern California and Oregon are also the lightest in color. In specimens from this region, the abdomen is usually white with black spots, as in eastern *S. albomaculata* (Fig. 65)

and the venter is as in *S. albomaculata* from the Rocky Mountains (Fig. 64). The smallest specimens from Texas are also often the darkest.

The male palpus shows a surprising amount of variation; however, the cline of variation here does not agree with the clines for color and size. The palpus of males from northern California (Fig. 38) is very similar to that of *S. fulva;* however, it has a larger white membrane on the ectal side of the palp at the inner side near the base of the embolus; the membrane covers more than one half the circle made by the embolus. Males from Arizona, Texas and Coahuila have a wide palpus (Figs. 39, 40). Unfortunately we do not have males from southern California or eastern Arizona, but they are expected to be intermediate in this character. Arizona and Texas specimens still have the large white membrane on the base of the embolus (Fig. 39), but this structure becomes smaller farther south (Fig. 40). Males from central and southern Mexico have a narrower palpus. The white membrane, however, is smaller (Figs. 40, 41), unlike that of the narrow California palpus. In Mexico the palpus still differs from that of *S. fulva* in that the embolus of *S. pulcher* describes an ellipse wider than high (Figs. 40, 41), while that of *S. fulva* is higher than wide.

Natural History. This species has been collected under rocks in desert in Oregon.

Distribution. Pacific coast states, southwest to Oaxaca. Map 10. In several papers Mello-Leitão refers to this species as having been found in South America. I assume he made a mistake in identification.

Records. Texas: Big Bend Natl. Pk.; Concho Co.; Kendall Co.; McCulloch Co.; Terrell Co. *Colorado:* Archuleta Co.; Piedra, 7000 ft. (H. and L. Levi). *New Mexico:* Otero Co. *Arizona:* Cochise Co.; Grand Canyon Natl. Pk.; Navajo Co.; Pima Co. *Oregon:* Deschutes Co.: 5 mi. S. of Redmond; Jackson Co.; Klamath Co.; Lake of the Woods; Lake Co.; Lake Albert. *California:* Eldorado Co.; Contra Costa Co.; Kings Canyon Natl. Pk.; Modoc Co.; Mono Co.; Plumas Co.; Riverside Co.; San Bernardino Co.; Shasta Co.; Sierra Co.; Siskiyou Co.; Tulare Co. *Coahuila:* 5 mi. W. of Saltillo; 20 mi. E. of San Pedro. *Chihuahua:* Santa Barbara; Primavera, 5500-6000 ft.; Matachic;

20 mi. W. of Matachic. *Durango:* Las Puentes, 700 ft.; Otinapa, 8200 ft. *Jalisco:* 20 mi. N. of La Quemada; Ajijic; Plan de Barrancas; west side of Lake Sayula; nr. Tequila. *Hidalgo:* 5 mi. S. of Zimapán. *Michoacan:* Tzararacua Falls nr. Uruapan. *Morelos:* Acatlipa; Cocoyoc; Alpoyeca; 10 mi. S. of Temixco. Coajomulco; Cuernavaca; 25 km. S. Cuernavaca. *Puebla:* Atlixco; 5 mi. N. of Tehuacán; Tehuacán; 12 mi. N. Acatlán; 7 mi. S. Tlacotepec; Tlacotepec. *Veracruz:* Perote. *Guerrero:* Hoajojutla; Taxco; Mexcala. *Oaxaca:* Oaxaca (many collections); Monte Alban.

Steatoda albomaculata (De Geer), new combination

Figures 56-65; Map 11.

Aranea albomaculata De Geer, 1778, Mémoires pour servir à l'histoire des Insectes, vol. 7, p. 257, pl. 15, figs. 2-4, ♀.

Eucharia corollata, C.L. Koch, 1837, Übersicht des Arachnidensystems, vol. 1, p. 8.

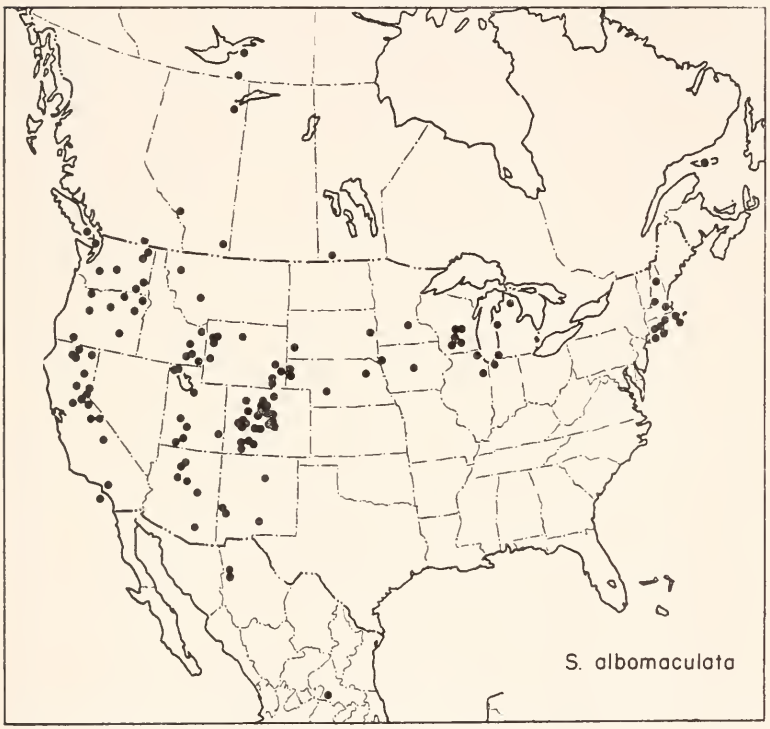
Asagena corollata, C.L. Koch, 1840, in Fürnrohr, Die Fauna von Regensburg, p. 401.

Steatoda corollata, Thorell, 1856, Recensio Critica Aranearum, p. 85; Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 21, pl. 4, fig. 5, ♀; 1902, The common spiders, p. 121, fig. 285, ♀; 1924, Canadian Ent., vol. 56, p. 124.

Lithyphantes corollatus, Thorell, 1869, On European spiders, p. 94. Emerton, 1876, Psyche, vol. 1, p. 130; 1877, Proc. Boston Soc. Nat. Hist., vol. 19, p. 70. Thorell, 1877, Bull. U.S. Geol. Surv. vol. 3, no. 2, p. 47. Keyserling, 1884, Die Spinnen Amerikas, vol. 2, pt. 1, p. 129, pl. 6, fig. 81, ♀, ♂. Marx, 1889, Proc. U.S. Natl. Mus., vol. 12, p. 522. Banks, 1901, Proc. Acad. Nat. Sci., Philadelphia, 1901, p. 579; 1895a, Jour. New York Ent. Soc., vol. 3, p. 84; 1895b, Ann. New York Acad. Sci., vol. 8, p. 432; 1902, Proc. U.S. Natl. Mus., vol. 25, p. 214. Bryant, 1908, Occas. Papers Boston Soc. Nat. Hist., vol. 7, p. 17. Banks, 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 182. Comstock, 1912, The spider book, p. 362, fig. 367, ♀. Emerton, 1920, Trans. Roy. Canadian Inst., vol. 12, p. 312. Crosby and Bishop, 1928, Mem. Cornell Agr. Exp. Sta., no. 101, p. 1039. Chamberlin, 1928, Canadian Ent., vol. 60, p. 93. Worley and Pickwell, 1931, Univ. Nebraska Studies, vol. 27, p. 27. Worley, 1932, Publ. Univ. Washington Biol., vol. 1, p. 25. Chickering, 1932, Papers Michigan Acad. Sci., vol. 15, p. 351. Chamberlin and Ivie, 1933, Bull. Univ. Utah, biol. ser., vol. 2, p. 8. Gertsch, 1935, Amer. Mus.

Novitates, no. 792, p. 21. Comstock, 1940, The spider book, rev. ed., p. 377, fig. 367,♀. Fox, 1940, Proc. Biol. Soc. Washington, vol. 53, p. 41. Probably not *Aranea corollata* Linnaeus, 1758.

Lithyphantes albomaculatus, Simon, 1914, Arachnides de France, vol. 6, p. 282. Wiehle, 1937, *in* Dahl, Die Tierwelt Deutschlands, pt. 33, p. 200, figs. 222-227,♀,♂. Gertsch, 1939, Amer. Mus. Novitates, no. 1032, p. 4. Roewer, 1942, Katalog der Aranaea, vol. 1, p. 405. Lowrie, 1942,



Map 11. American distribution of *Steatoda albomaculata* (De Geer).

Bull. Chicago Acad. Sci., vol. 6, p. 169; 1948, Ecology, vol. 29, p. 338. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 78, figs. 47-50,♀,♂. Kurata, 1949, Canadian Ent., vol. 81, p. 127. Levi and Levi, 1951, Zoologica, vol. 36, p. 220. Kaston, 1953, How to know the spiders, p. 163, fig. 407,♀. Locket and Millidge, 1953, British spiders, vol. 2, p. 55, fig. 37,♀,♂. Levi and Field, 1954, Amer. Mid-

land Nat., vol. 51, p. 444. Kaston, 1955, Trans. Illinois Acad. Sci., vol. 47, p. 166.

Types. The type came from the shore of the Baltic Sea.

Description. Carapace, sternum, legs, dark brown. Abdomen black often with a white line along anterior edge, venter black with white marks (Fig. 64). Eastern specimens may have abdomen white or white with black marks, sometimes in the form of a series of anterior pointing triangles making a median dorsal black line. Eyes subequal in size, laterals usually slightly separated from each other. The endites of the male have tubercles. Epigynum illustrated by Figure 58, male palpus by Figures 59-61. Total length of females, 4.0-8.0 mm. A female from Colorado measured: total length, 6.1 mm. Carapace 2.0 mm. long, 1.8 mm. wide. First femur, 2.6 mm.; patella and tibia, 2.7 mm.; metatarsus, 2.1 mm.; tarsus, 1.0 mm. Second patella and tibia, 2.2 mm.; third, 1.8 mm.; fourth, 2.6 mm. Total length of males, 4.3-6.8 mm. A male from Colorado measured: total length, 4.8 mm. Carapace 2.2 mm. long, 1.6 mm. wide. First femur, 2.9 mm.; patella and tibia, 3.5 mm.; metatarsus, 2.6 mm.; tarsus 1.1 mm. Second patella and tibia 2.6 mm.; third, 2.0 mm.; fourth, 3.2 mm.

Variation. The coloration in eastern specimens is light (Fig. 65) while that of western ones is usually dark, the abdomen of the latter usually being black with only a white line along the anterior edge and a ventral white mark. The shape of the epigynum is quite variable. The median lobe may be much wider than long or longer than wide. The tip of the projecting radix of the palpus varies in shape. However these differences are apparently not geographic.

Natural History. This species is very common in the Colorado mountains where it is found under stones in dry, open, areas up to timberline and down to the foothills where *Latrodectus* replaces it in similar habitats. Several spiders with numerous egg sacs are found together, along with the remains of insects, often ants. Kaston (1948) records egg sacs to be 4.5-8.0 mm. in diameter containing 20-33 tan eggs. In Europe this species is also black in color in the mountains, although black individuals may also be found in other areas (Wiehle, 1937).

Distribution. Southern England, Europe, North Africa, Siberia, China, Kamchatka (Wiehle, 1937). Common in western

states and northeastern states. South to central Mexico, north to Great Slave Lake; South America. Map 11. Judging by its wide distribution in North America and its color variation in different parts of the range, this species is native to North America as well as Europe.

Records. Quebec: (Emerton, 1924). *Manitoba:* (Emerton, 1920). *Northwest Territories:* (Kurata, 1949). *Alberta:* (Emerton, 1920); Medicine Hat; Lake Athabasca. *British Columbia:* (Emerton, 1920); Cascade; Mt. Arrowsmith. *New Hampshire:* Cheshire Co. *Massachusetts:* Barnstable Co.; Dukes Co.; Essex Co. *Connecticut:* New London Co. (Kaston, 1948). *New York:* (Crosby and Bishop, 1928); Nassau Co.; Suffolk Co. *Michigan:* (Chickering, 1932; Lowrie, 1948); Oceana Co. *Indiana:* (Lowrie, 1942, 1948). *Wisconsin:* (Levi and Field, 1954); Dane Co.; Iowa Co.; Sauk Co. *Illinois:* (Kaston, 1955); Kankakee Co. *Minnesota:* Hennepin Co. *Iowa:* Ames; Sioux City. *South Dakota:* Brookings; Custer Co. *Nebraska:* (Worley and Pickwell, 1931); Boone Co.; Scotts Bluff Co. *Montana:* (Gertsch, 1939); Helena. *Wyoming:* (Levi and Levi, 1951); Cheyenne; Goshen Co.; Lincoln Co.; Niobara Co.; Teton Co.; Washakie Co. *Colorado:* (Banks, 1895b; Fox, 1940); Archuleta Co.; Boulder Co.; Chaffee Co.; El Paso Co.; Gilpin Co.; Gunnison Co.; Hinsdale Co.; Jefferson Co.; Lake Co.; Larimer Co.; Mineral Co.; Rio Grande Co.; Routt Co.; Teller Co. *New Mexico:* Catron Co.; Otero Co.; San Miguel Co. *Idaho:* Bannock Co.; Bear Lake Co.; Bingham Co.; Fremont Co.; Power Co. *Utah:* (Chamberlin and Ivie, 1933; Fox, 1940); Bryce Canyon Natl. Pk.; Kane Co.; Millard Co.; San Juan Co.; Sevier Co. *Arizona:* (Banks, 1902); Flagstaff; Grand Canyon Natl. Pk.; Navajo Co.; Pima Co. *Washington:* (Worley, 1932); Mt. Ranier Natl. Pk.; San Juan Co.; Stevens Co.; Walla Walla; Whitman Co. *Oregon:* Baker Co.; Deschutes Co.; Harney Co.; Hood River Co.; Jackson Co.; Umatilla Co.; Wallowa Co.; Wheeler Co. *California:* Alpine Co.; Eldorado Co.; Inyo Co.; Lassen Co.; Los Angeles Co.; Modoc Co.; Mono Co.; Nevada Co.; Placer Co.; Sacramento Co.; Siskiyou Co.; Yosemite Natl. Pk.; Yuba Co. *Chihuahua:* Los Canoas Babîcora; 7700 ft. summit NE of San José Babícora; Matachic. *San Luis Potosí:* 12 mi. W. of Arriaga.

Steatoda americana (Emerton), new combination

Figures 66-69; Map 12.

Asagena americana Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 23, pl. 4, fig. 6,♂. Keyserling, 1886, Die Spinnen Amerikas, vol. 2, pt. 2, p. 2 pl. 11, fig. 135,♂. Marx, 1889, Proc. U.S. Natl. Museum, vol. 12, p. 525. Simon, 1894, Histoire naturelle des Araignées vol. 1, p. 574, fig. 586. Banks, 1895, Jour. New York Ent. Soc., vol. 3, p. 84; 1895, Ent. News, vol. 6, p. 205. Emerton, 1902, The common spiders, p. 122, fig. 287,♀. Banks, 1904, Proc. Acad. Nat. Sci. Philadelphia, vol. 56, p. 653; 1907, Indiana Dept. Geol. Nat. Resources, 31st Rept., p. 739; 1908, Proc. Ent. Soc. Washington, vol. 9, p. 5; 1910, Bull. U.S. Natl. Mus., no. 72, p. 22; 1911, Proc. Acad. Nat. Sci. Philadelphia, vol. 63, p. 445. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 170. Comstock, 1912, The spider book, p. 364, fig. 369,♀. Emerton, 1913, Appalachia, vol. 12, p. 155. Barrows, 1918, Ohio Jour. Sci., vol. 18, p. 302. Emerton, 1920, Trans. Roy. Canadian Inst., vol. 12, p. 312. Bishop, 1925, Bull. New York State Mus., no. 260, p. 66, fig. 1,♂. Bishop and Crosby, 1926, Jour. Elisha Mitchell Sci. Soc., vol. 41, p. 176. Crosby and Bishop, 1928, Mem. Cornell Agr. Exp. Sta., no. 101, p. 1039. Chamberlin, 1928, Proc. Biol. Soc. Washington, vol. 41, p. 179. Worley and Pickwell, 1931, Univ. Nebraska Studies, vol. 27, p. 25. Worley, 1932, Publ. Univ. Washington Biology, vol. 1, p. 23. Banks, Newport and Bird, 1932, Publ. Univ. Oklahoma, Biol. Surv., vol. 4, no. 1, p. 21. Chickering, 1934, Papers Michigan Acad. Sci., vol. 19, p. 578. Fox, 1940, Proc. Biol. Soc. Washington, vol. 53 p. 40. Comstock, 1940, The spider book, rev. ed., p. 379, fig. 369,♀. Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 37. Muma, 1945, Bull. Univ. Maryland Agr. Exp. Sta., no. A38, p. 24. Muma and Jeffers, 1945, Ann. Ent. Soc. America, vol. 38, p. 248. Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 22. Levi and Field, 1954, Amer. Midland Nat., vol. 51, p. 442. Kaston, 1955, Trans. Illinois Acad. Sci., vol. 47, p. 166. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 73, figs. 25-29,♀,♂. Kaston, 1953, How to know the spiders, p. 163, fig. 406,♀. Elliott, 1953, Proc. Indiana Acad. Sci., vol. 62, p. 308. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 753.

Asagena dubia, Roewer, 1942, Katalog der Araneae, vol. 1, p. 397. Probably not *Herpyllus dubia* Hentz.

Types. Male holotype from garden fence in Boston, Mass., May 30, in the Museum of Comparative Zoology.

Description. Carapace, sternum brown; legs yellow-brown. Abdomen black, often with a pair of white spots on posterior

portion of dorsum. Anterior median eyes sometimes slightly smaller than others, almost their diameter apart, three-quarters diameter from laterals. Posterior eyes one diameter apart, one diameter from laterals. Tooth on anterior margin of male chelicerae indistinct. Males with femora swollen, often with ventral spines on first femora and tibia, but these may be absent. Usually with a thorn on distal end of second femur. Epigynum illustrated by Figure 67, male palpus by Figure 68. Total length of females 3.5-4.7 mm. A female from Wisconsin measured: total length, 4.0 mm. Carapace 1.6 mm. long, 1.3 mm. wide.

Map 12. Distribution of *Steatoda americana* (Emerton).

First patella and tibia, 1.5 mm.; second, 1.2 mm.; third 1.0 mm. Fourth femur, 1.2 mm.; patella and tibia, 1.6 mm.; metatarsus, 0.7 mm.; tarsus, 0.6 mm. Total length of males, 3.2-4.4 mm. A male from Wisconsin measured: total length, 4.4 mm. Carapace 2.2 mm. long, 1.6 mm. wide. First patella and tibia, 1.7 mm.; second, 1.2 mm.; third, 1.4 mm. Fourth femur, 1.5 mm.; patella and tibia, 1.7 mm.; metatarsus, 1.2 mm.; tarsus, 0.7 mm.

Natural History. This species is found in leaf litter, under stones, under loose bark of logs and in moss; it has also been found in Wisconsin sweeping grass and vegetation in woods. It has been found with three spherical, transparent, egg sacs, 4-5

mm. in diameter, containing 22-33 light yellow eggs (Kaston, 1948). Muma and Jeffers (1945) have found it in nests of the wasp *Sceliphron*. It has also been reported from other wasp nest collections.

Distribution. United States and southern Canada, except California and Oregon, south to Hidalgo.

Records. Ontario: Rockport. *British Columbia:* (Emerton, 1920). *Maine:* Cumberland Co. *New Hampshire:* (Emerton, 1913). *Vermont:* Chittenden Co. *Rhode Island:* (Fox, 1940). *Connecticut:* (Kaston, 1948). *New York:* (Crosby and Bishop, 1928); Bronx; Onondaga Co.; Suffolk Co. *New Jersey:* Bergen Co. *Maryland:* (Muma, 1945). *District of Columbia:* Washington. *Virginia:* Fairfax Co. *West Virginia:* (Bishop and Crosby, 1924); Pocahontas Co. *North Carolina:* (Banks, 1911; Bishop and Crosby, 1926); Swain Co. *Georgia:* (Chamberlin and Ivie, 1944). *Florida:* (Banks, 1904). *Alabama:* (Archer, 1946). *Ohio:* (Barrows, 1918); Columbiana Co.; Cuyahoga Co. *Michigan:* (Chickering, 1934). *Indiana:* (Elliott, 1953); Porter Co. *Tennessee:* Roane Co. *Wisconsin:* (Levi and Field, 1954); Crawford Co.; Door Co.; Grant Co.; Richland Co.; Vernon Co. *Illinois:* (Kaston, 1955); Randolph Co. *Missouri:* (Banks, 1895); Crawford Co.; St. Louis. *Nebraska:* (Worley and Pickwell, 1931). *Oklahoma:* Cleveland Co. *Texas:* San Antonio. *Colorado:* Archuleta Co.; Denver. *New Mexico:* Catron Co.; Otero Co. (9-12000 ft.). *Idaho:* Bear Lk. Co. *Utah:* (Chamberlin, 1928); Salt Lake City; Zion Natl. Pk. *Arizona:* Mohave Co. *Washington:* (Worley, 1932). *Oregon:* Salem. *Sonora:* 27 mi. S. of Nogales. *Hidalgo:* S. of Jacala, July 20, 1956 (V. Roth, W. J. Gertsch).

Steatoda septemmaculata (Keyserling), new combination

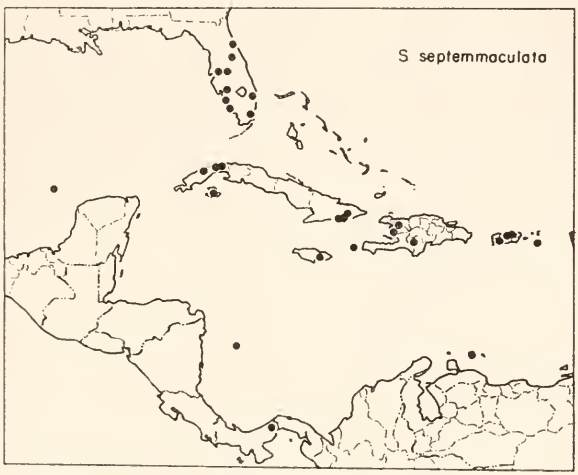
Figures 70-73; Map 13.

Lithyphantes septemmaculatus Keyserling, 1884, Die Spinnen Amerikas, vol. 2, no. 1, p. 141, pl. 6, fig. 88, ♀. van Hasselt, 1887, Tijdschr. Ent., vol. 30, p. 234. Marx, 1889 Proc. U.S. Natl. Mus., vol. 12, p. 522. Banks, 1904, Proc. Acad. Nat. Sci. Philadelphia, vol. 56, p. 653; 1910, Bull. U.S. Natl. Mus. no. 72, p. 21. Petrunkevitch, 1911, Bull Amer. Mus. Nat. Hist., vol. 29, p. 183; 1930, Trans. Connecticut Acad. Sci., vol. 30, p. 169, figs. 6, 7, ♀. Bryant, 1940, Bull. Mus. Comp. Zool., vol.

86, p. 304. Roewer, 1942, Katalog der Araneae, vol. 1, p. 408. Bryant, 1942, Bull. Mus. Comp. Zool., vol. 89, p. 337; 1945, Trans. Connecticut Acad. Sci., vol. 36, p. 204, pl. 1, fig. 7, 9, ♂; 1948, Bull. Mus. Comp. Zool., vol. 100, p. 375. ? Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 79.

Types. Syntypes from "Denver in Columbia" collected by Marx, and also from Enterprise, Florida, in the United States National Museum. Marx's labels are commonly wrong and the Denver locality is undoubtedly an error.

Description. Carapace, sternum, legs orange. Femora dusky. Abdomen purple-black with seven white spots on dorsum (Fig. 70), two of them above spinnerets. Eyes subequal in size. An-



Map 13. Distribution of *Steatoda septemmaculata* (Keyserling).

terior median eyes one diameter apart, less than one diameter from laterals. Posterior medians one diameter apart, one and one-half diameters from laterals. Laterals slightly separated from each other. Chelicerae and maxillae of male modified; the former lacking teeth. Epigynum illustrated by Figure 72, male palpus by Figure 73. Total length of females 2.5-3.2 mm. A female from Florida measured total length 2.5 mm. Carapace 1.10 mm. long, 0.88 mm. wide. First patella and tibia, 1.00 mm.; second, 0.89 mm.; third, 0.75 mm. Fourth femur, 1.04 mm.;

patella and tibia, 1.18 mm.; metatarsus, 0.62 mm.; tarsus, 0.47 mm. Total length of males 1.8-3.4 mm. A male from Florida measured total length, 3.0 mm. Carapace 1.78 mm. long, 1.11 mm. wide. First patella and tibia, 1.26 mm.; second 1.15 mm.; third, 0.98 mm. Fourth femur, 1.28 mm.; patella and tibia, 1.35 mm.; metatarsus, 0.84 mm.; tarsus, 0.60 mm.

Natural History Petrunkevitch (1930) found this species on the undersides of old coconut shells and in cactus fields in Puerto Rico.

Distribution. Florida, Panama, West Indies. (Map 13.) Kaston (1948) reported a female found in Litchfield, Connecticut. This has presumably been imported, or it is an erroneous record. The specimen could not be found.

Records. Florida: (Banks, 1904; Bryant, 1945) Collier Co.; De Soto Co.; Hillsborough Co.; Orange Co.; Polk Co. *Yucatan:* Cayo Arenas. *Panama:* Santa Rosa (Colón); Ensenada. *Isla de Providencia. Cuba:* (Bryant, 1940); Habana; Cabañas; Daiquiri; Pinar del Río; Marianao. *Jamaica:* Western Kingston. *Navassa Isl. Hispaniola:* (Bryant, 1948). *Puerto Rico:* (Petrunkevitch, 1930). *Virgin Islands:* (Bryant, 1942). *Lesser Antilles:* (van Hasselt, 1887).

Steatoda grossa (C.L. Koch)

Figures 74, 83-85; Map 14.

Theridion grossum C.L. Koch, 1838, Die Arachniden, vol. 4, p. 112, fig. 321, ♀.

Steatoda grossa, C.L. Koch, 1851. Übersicht des Arachnidensystems, pt. 5, p. 17.

Theiridion nitidum Holmberg, 1876, An. Agr. Argentina, vol. 4, p. 72.

Theridion domesticum Holmberg, 1876, *op. cit.*

Steatoda pusulosa Keyserling, 1877, Verhandl. zool. bot. Gesell. Wien., vol. 27, p. 579, pl. 14, fig. 7, 8, ♀, ♂.

Lithyphantes grossa, Pavesi, 1878, Ann. Mus. Civ. Genova, vol. 11, p. 371.

Teutana grossa, Simon, 1881, Les Arachnides de France, vol. 5, p. 164. Banks, 1898, Proc. California Acad. Sci., 3rd ser., vol. 1, p. 238, F.O.P. Cambridge, 1902, Biologia Centrali Americana, Araneidea, vol. 2, p. 374, pl. 35, fig. 9, 10, ♀, ♂. Banks, 1909, Proc. Acad. Nat. Sci. Philadelphia, vol. 61, p. 205. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 189. Emerton, 1911, Trans. Connecticut Acad. Sci., vol. 16, p. 387, fig. 2, ♂. Chamberlin, 1919, Jour. Ent. Zool., vol. 12,

p. 25. Reimoser, 1939, Ann. Naturhist. Mus. Wien, vol. 50, p. 344. Fox, 1940, Proc. Biol. Soc. Washington, vol. 53, p. 42. Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., vol. 6, no. 3, p. 12. Roewer, 1942, Katalog der Araneae, vol. 1, p. 414. Branch, 1942, Bull. South. California Acad. Sci., vol. 41, p. 138. Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 21. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 86, figs. 60-62, ♀, ♂. Schenkel, 1950, Verhandl. Naturf. Gesell. Basel, vol. 61, p. 52.

Teutana nitida, Keyserling, 1882, Die Spinnen Amerikas, vol. 2, pt. 1, p. 124, pl. 6, fig. 79, ♀, ♂.

Teutana zonata Keyserling, 1882, *op. cit.*, p. 127, pl. 6, fig. 80, ♂. Banks, 1898, Proc. California Acad. Sci., 3rd ser. vol. 1, p. 238. O.P. Cambridge, 1902, Biologia Centrali Americana, Araneidea, vol. 1, p. 306, pl. 35, fig. 7, 8, ♀, ♂. NEW SYNONYMY.

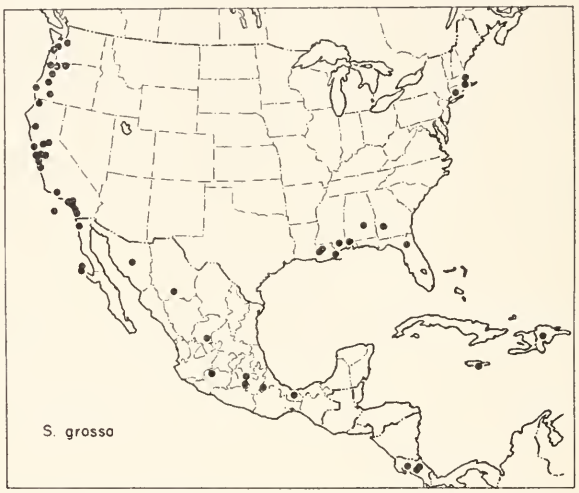
Asagena zonata, F.O.P., Cambridge, 1902, *ibid*, vol. 2, p. 378. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 171. Roewer, 1942, Katalog der Araneae, vol. 1, p. 397, Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 757. NEW SYNONYMY.

Teutana modesta Bryant, 1948, Bull. Mus. Comp. Zool., vol. 100, p. 375, figs. 49, 51, ♀. NEW SYNONYMY.

Types. The types of *Theridion grossum* from Peloponnesus peninsula and Germany. The types of *Theridion nitidum* and *Theridion domesticum* Holmberg from Argentina are lost. The types of *Steatoda pusulosa* Keyserling from Uruguay. Male type of *Teutana zonata* Keyserling from Mexico in the Muséum National Histoire Naturelle in Paris. Female holotype of *Teutana modesta* Bryant from the Cordillera Central, Valle Nuevo, 7000 ft., Dominican Republic in the Museum of Comparative Zoology.

Description. Carapace, sternum, legs dark orange. Abdomen purple-black, with an indistinct light line around anterior margin and several indistinct light patches on dorsum or with pattern as in *S. triangulosa*. Eyes subequal in size. Anterior eyes separated by one-third their diameter. Posterior medians separated by one-half their diameter, by one diameter from laterals. Chelicerae of males swollen, with a short thick fang. Epigynum variable, sometimes with a wide septum (Fig. 84) sometimes with septum almost missing (Fig. 85). Male palpus illustrated by Figure 74. Total length of females 5.9-10.5 mm. A female from California measured: total length, 8.6 mm. Carapace 3.2 mm. long, 2.7 mm. wide. First femur, 4.5 mm.; patella and tibia.

5.6 mm.; metatarsus, 4.3 mm.; tarsus, 1.9 mm. Second patella and tibia, 4.0 mm.; third, 3.2 mm., fourth, 4.5 mm. Total length of males 4.1-7.2 mm. A male from California measured: total length, 6.5 mm. Carapace 3.1 mm. long, 2.3 mm. wide. First femur, 4.7 mm.; patella and tibia, 5.5 mm.; metatarsus, 4.6 mm.; tarsus, 1.8 mm. Second patella and tibia, 4.1 mm.; third, 3.2 mm.; fourth, 4.7 mm.



Map 14. North and Central American distribution of *Steatoda grossa* (C.L. Koch).

Natural History. Branch (1942) raised *S. grossa* in the laboratory, feeding it on *Drosophila* and house flies. This species seems to be common in cities in North America. Archer (1946) reports that it lives in brick piles and under loose bricks and that it preys on *Latrodectus mactans* (Fabricius), the black-widow spider.

Distribution. Cosmopolitan. In the United States, along the coasts only (Map 14). The proximity of this species to man would suggest that it has been introduced recently into North America.

Records. Massachusetts: (Emerton, 1911). *Rhode Island:* Providence. *Connecticut:* (Kaston, 1948). *Georgia:* Daugherty

Co. *Florida:* Alachua Co. *Alabama:* Mobile; (Archer, 1946). *Mississippi:* Forrest Co. *Louisiana:* East Baton Rouge Par.; Orleans Par.; West Baton Rouge Par. *Washington:* Olympia; Pacific Co.; Seattle. *Oregon:* Corvallis; Curry Co.; Jackson Co.; Eugene; Hood River Co.; Portland; Tillamook Co. *California:* (Chamberlin and Ivie, 1944; Schenkel, 1950); Alameda Co.; Del Norte Co.; Los Angeles Co.; Marin Co.; Monterey Co.; Mendocino Co.; Sacramento, San Diego Co.; San Francisco; San Nicolas Isl.; Santa Barbara; Yolo Co. *Chihuahua:* Santa Barbara. *Baja California:* Isl. Cedros; Isl. Natividad. *Sonora:* (Banks, 1898). *Zacatecas:* 10 mi. E. of Zacatecas. *Puebla:* Tehuacán. *Distrito Federal:* San Gerónimo; San Angel; Coayacan; Mexico (in house). *Morelos:* Cuernavaca. *Michoacan:* Zamora. *Veracruz:* Los Naranjos. *Costa Rica:* (Banks, 1909; Reimoser, 1939). *Jamaica:* St. Andrew Par. *Peru:* Arequiba; Acomayo (Huanuco); Tingo María; Lima. *Brazil:* Minas Gerais; Min. Serinha Diamantina. *Argentina:* (Keyserling, 1886); Salta.

Steatoda triangulosa (Walckenaer)

Figures 75, 76, 80-82; Map 15.

Aranea triangulosa Walckenaer, 1892, Faune Parisienne, vol. 2, p. 207.

Theridion triangulifer, Walckenaer, 1895, Tableau des Aranéides, p. 75, pl. 8, fig. 73, 74.

Theridion serpentinum Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 273, pl. 9, fig. 2; 1875, The spiders of the United States, p. 144, pl. 16, fig. 2.

Steatoda triangulifera, Simon, 1873, Mem. Soc. Roy. Sci. Liège, vol. 5, p. 116.

Steatoda triangulosa, Thorell, 1873, Remarks on synonyms of European spiders, p. 505. Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 22, fig. 6, ♂. Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia, p. 31. Emerton, 1902, The common spiders, p. 121, fig. 286, ♀.

Teutana triangulosa, Simon, 1881, Les Arachnides de France, vol. 5, p. 163. Keyserling, 1884, Die Spinnen Amerikas, vol. 2, pt. 1, p. 122, pl. 6, fig. 78, ♀, ♂. Marx, 1889, Proc. U.S. Natl. Mus., vol. 12, p. 521. Banks, 1895, Ent. News, vol. 6, p. 205; 1896, Jour. New York Ent. Soc., vol. 4, p. 191; 1899, Proc. Ent. Soc. Washington, vol. 4, p. 189; 1900, Proc. Acad. Nat. Sci. Philadelphia, p. 533. Montgomery, 1903, *ibid.*, p. 112. Scheffer, 1905, Trans. Kansas Acad. Sci., vol. 19, p. 192. Bryant,

1908, Occas. Papers Boston Soc. Nat. Hist., vol. 7, p. 17. Banks, 1910, Bull. U.S. Natl. Mus., no. 72, p. 21; 1911, Proc. Acad. Nat. Sci. Philadelphia, vol. 63, p. 445. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 190. Comstock, 1912, The spider book, p. 361, figs. 364, 365, ♀. Barrows, 1918, Ohio Jour. Sci., vol. 18, p. 304. Bishop and Crosby, 1926, Jour. Elisha Mitchell Sci. Soc., vol. 41, p. 181, Crosby and Bishop, 1928, Mem. Cornell Agr. Exp. Sta., no. 101, p. 1041. Worley and Pickwell, 1931, Univ. Nebraska Studies, vol. 27, p. 29. Banks, Newport and Bird, 1932, Publ. Univ. Oklahoma, Biol. Surv., vol. 4, no. 1, p. 22. Wiehle, 1937, *in* Dahl, Die Tierwelt Deutschlands, pt. 33, p. 198, figs. 217-221, ♀, ♂. Stiles and Detwiler, 1938, Proc. Iowa Acad. Sci., vol. 45, p. 286. Comstock, 1940, The spider book, rev. ed., p. 376, figs. 364-365, ♀. Fox, 1940, Proc. Biol. Soc. Washington, vol. 53, p. 42. Roewer, 1942, Katalog der Araneae, vol. 1 p. 416. Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 46. Muma, 1945, Bull. Univ. Maryland Agr. Exp. Sta., no. A38, p. 27. Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 21. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 86, figs. 57-59, ♀, ♂. Kaston, 1953, How to know the spiders, p. 165, fig. 413, ♀. Elliott, 1953, Proc. Indiana Acad. Sci., vol. 62, p. 309. Levi and Field, 1954, Amer. Midland Nat., vol. 51, p. 444. Kaston, 1955, Trans. Illinois Acad. Sci., vol. 47, p. 166.

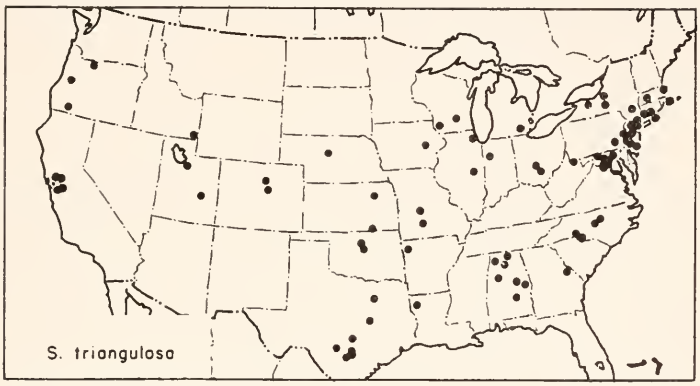
Theridion saylori Fox, 1940, Proc. Biol. Soc. Washington, vol. 53, p. 43, fig. 1, ♀.

Types. Types of *Aranea triangulosa* from Paris, France. Type of *Theridion serpentinum* from Georgia is lost. Type of *Theridion saylori* from Ozark Lake, Missouri in the United States National Museum.

Description. Carapace, sternum orange-yellow; legs yellow. Abdomen purplish brown with white spots on dorsum (Fig. 82) and towards sides. Eyes subequal or anterior medians smaller. Anterior median eyes separated by two-thirds their diameter, by one-third to two-thirds from laterals. Posterior medians two-thirds to one diameter apart, one diameter from laterals. Epigynum illustrated by Figure 81, male palpus by Figure 76. Total length of females, 3.6-5.9 mm. A female from Massachusetts measured: total length, 5.1 mm. Carapace 1.9 mm. long, 1.8 mm. wide. First femur, 3.0 mm.; patella and tibia, 3.8 mm.; metatarsus, 2.6 mm.; tarsus, 1.3 mm. Second patella and tibia, 2.4 mm.; third, 1.6 mm.; fourth, 2.7 mm. Total length of males 3.5-4.7 mm. A male from Massachusetts measured: total length, 4.7 mm. Carapace 2.3 mm. long, 1.8 mm. wide. First femur

3.2 mm.; patella and tibia, 3.7 mm.; metatarsus, 2.4 mm.; tarsus, 2.0 mm. Second patella and tibia, 2.5 mm.; third, 2.0 mm.; fourth, 2.7 mm.

Natural History. This species is locally common in and on houses. In museums it may infest dermestid beetle cultures. Wiehle (1937) reports that it lives in houses in the northern part of its range in Europe, under stones and on walls in the southern part of the range. This agrees with Archer's (1946) observations in the southern United States. Montgomery (1903) observed mating of this species.



Map 15. North American distribution of *Steatoda triangulosa* (Walckenaer).

Distribution. Central and southern Europe, southern Russia, Mediterranean, St. Helena (Wiehle, 1937). United States. Map 15. South America. The city dwelling habit would suggest that this species has been introduced to North America recently.

Records. Massachusetts: (Bryant, 1908); Bristol Co.; Springfield. *Connecticut:* (Kaston, 1948). *New York:* (Banks, 1896; Crosby and Bishop, 1928) Rochester; Bronx; Manhattan; Brooklyn. *New Jersey:* (Fox, 1940); Bergen Co.; Camden Co.; Mercer Co. *Pennsylvania:* Lancaster; Northampton Co.; Philadelphia. *Maryland:* (Keyserling, 1884; Muma, 1945). *District of Columbia:* (Fox, 1940). *Virginia:* Fairfax Co. *West Virginia:* Monongahela Co. *North Carolina:* (Banks, 1911; Fox, 1940); Mecklenburg Co.; Union Co. *South Carolina: Georgia:* (Hentz,

1850; Chamberlin and Ivie, 1944). *Alabama:* (Archer, 1946); Colbert Co.; Tallapoosa Co. *Louisiana:* (Banks, 1899). *Ohio:* (Hentz, 1875; Barrows, 1918). *Michigan:* Washtenaw Co. *Indiana:* (Elliott, 1953). *Wisconsin:* (Levi and Field, 1954). *Illinois:* Cook Co.; Urbana. *Iowa:* (Stiles et al. 1938). *Missouri:* (Banks, 1895). *Arkansas:* Washington Co. *Nebraska:* (Worley and Pickwell, 1931). *Kansas:* (Scheffer, 1905); Cowley Co. *Oklahoma:* (Banks et al., 1932); Payne Co. *Texas:* Atascosa Co.; Austin; Dallas; Kerr Co.; McLennan Co.; San Antonio. *Colorado:* Boulder; Denver. *Idaho:* Bear Lake. *Utah:* Emery Co.; Salt Lake City. *Oregon:* Jackson Co.; Lane Co.; Wasco Co. *California:* Alameda Co.; Solano Co.

Steatoda castanea (Clerck)

Figures 77-79

Araneus castaneus Clerck, 1757, Aranei Suecici, p. 49, pl. 3, fig. 3.
Teutana castanea, Wiehle, 1937, *in* Dahl, Die Tierwelt Deutschlands, pt. 33, p. 195, figs. 205-211, ♀, ♂. Roewer 1942, Katalog der Araneae, vol. 1, p. 415.

One female has been collected at St. Thomas, Ontario, probably in a greenhouse. It has not become established in this region.

Distribution. Europe. Turkestan (Wiehle, 1937).

Steatoda bipunctata group

The group is represented by a series of closely related species with the eastern *Steatoda borealis* at one extreme, the European *S. bipunctata* at the other. In North America they present a series of mostly allopatric forms, each slightly different from the preceding. The last two of these species (*grandis, americana*) overlap one of the preceding (*hespera*). Furthermore, these last two are sympatric over part of their range. An attempt was made to cross one female *S. hespera* with males of *S. borealis* in the laboratory. No egg sac was produced. This, however, should be repeated.

Description. The coloration, size, proportions of all species are about the same. The carapace is yellow to red-brown, sternum and legs brown, coxae lighter brown. Dorsum of abdomen

dark brown to purplish black with a median white line and an anterior marginal line which continues on sides (Fig. 91). Venter light with two dark marks, or rarely all yellow or all dark (Fig. 90). Short spines covering thorax, more distinct in male. Carapace of males more rugose. Anterior median eyes larger (about 1.3 diameter) than others. Anterior medians two-thirds diameter apart, less than one-fourth diameter from laterals. Posterior medians separated by about one diameter, slightly closer to laterals. Laterals slightly separated from each other in many species. Epigynum similar in all species. Internal genitalia heavily sclerotized, not very useful in differentiating species. Male palpus with large radix (R in Figs. 153-154). A female *Steatoda borealis* from Wisconsin measured: total length, 4.8 mm. Carapace 1.8 mm. long, 1.6 mm. wide. First femur, 2.2 mm.; patella and tibia, 2.6 mm.; metatarsus, 1.6 mm.; tarsus, 1.0 mm. Second patella and tibia, 1.8 mm.; third, 1.4 mm.; fourth, 2.2 mm. A male from Wisconsin measured: total length, 4.5 mm. Carapace 2.0 mm. long, 1.6 mm. wide. First femur, 2.3 mm.; patella and tibia, 2.9 mm.; metatarsus, 1.9 mm.; tarsus, 1.1 mm. Second patella and tibia, 2.0 mm.; third, 1.6 mm.; fourth, 2.2 mm.

Variation. Three species are polymorphic (*S. atascadera, S. mexicana, S. grandis*). The genitalia of *S. atascadera* seem more variable in that part of its range where no other species of the *S. bipunctata* group are found, than in the northern part of its range where *S. hespera* is also found. The male palpi of *S. grandis* are quite uniform in structure, but the epigyna are extremely variable. Both the palpi and epigyna of *S. mexicana* are variable. Where collected together, *S. grandis* and *S. mexicana* always are quite distinct; however females from many localities may be difficult to place. It is assumed that in these latter localities only one or the other species occurs.

The question may be raised here whether *S. borealis* and *S. hespera* are two species or subspecies. There is no overlap in the two groups and the distribution would indicate that only one species is involved. However males and females of the two species in the Rocky Mountain region are always easy to place in one species or another, while some female *S. hespera* from the West Coast appear much more like *S. borealis.* In other words the species seem more distinct along the common border

of their range than in other parts of it, which would indicate that we are dealing with two species.

Natural History. The species of *Steatoda* live under bark, in crevices of rocks, sometimes under stones. They are common in buildings where they build small webs in corners; however, during daytime the spiders stay hidden in crevices, coming out to the web in the evening. Females and males may inhabit the same web. In captivity slight vibration of flies in the web, or sometimes only the presence of a dead fly in the web, brought the spiders out of their retreats. Kaston (1948) described the egg sac of *S. borealis* as being "loosely woven, so that the ivory to pale pink eggs show through the brownish white threads. The shape is approximately spherical 5-6.5 mm. in diameter and I counted in four egg sacs, 37, 47, 76, and 95 eggs respectively."

Distribution. This group may be mainly holarctic in distribution. The male *Steatoda brasiliana* Keyserling from Brazil may be an introduced form.

Key to females of the Steatoda bipunctata *group*

Note that figures were drawn with the epigynum lying flat, thus from a slightly anterior position of the abdomen.

1. Raised anterior median lobe of epigynum wider than long (Fig. 113) 2
1. Raised anterior median lobe as long as wide, or longer than wide (Fig. 93, 105, 109) 4
2. Anterior arms of depression pointing straight anterior (Figs. 107-109), California coast range (Map 17) ..... *atascadera*
2. Arms of depression pointing slightly to sides (Figs. 111, 113, 115) 3
3. Posterior portion of depression swollen and wider than arms (Figs. 117, 118). East of Rocky Mountains to Alaska (Map 19) ... *borealis*
3. Posterior portion of depression as wide as arms (Figs. 111, 113, 115) Western United States to southern British Columbia (Map 19) ..... *hespera*
4. Raised anterior median lobe as wide as long (Figs. 107, 109). California coast range (Map 17) ..... *atascadera*
4. Raised anterior median lobe longer than wide 5
5. Found in southern California (Map 17) .... *palomara*
5. Not found in southern California 6
6. With a large swollen posterior lip and swollen areas on each side of depression (Fig. 89) ..... *bipunctata*
6. Lacking swollen areas on each side of depression 7

7. Openings in a deep depression on sides of a very narrow septum (Figs. 93-97). Depression often with material difficult or impossible to remove. Western United States (Map 17) ..... *grandis*
7. Openings in a shallower depression, septum wider (Figs. 99-103). Material in depression easily removed. Western United States and Mexico (Map 18) .... *mexicana*

Key to males of the Steatoda bipunctata *group*

Note that figures of the palpus in mesal view were drawn with the radix lying flat, thus from a slightly anterior view.

1. Radix with a well-developed median lobe (Figs. 148, 153). East of Rocky Mountains to Alaska (Map 19) ..... *borealis*
1. Radix lacking median lobe (Figs. 119, 129, 142, 155) 2
2. Radix enclosing an area, the diameter of which is less, equal or only slightly more than the greatest width of radix (Figs. 119, 155) ... 3
2. Radix enclosing an area, the diameter of which is much greater than the width of the radix (Figs. 129, 145) 4
3. Embolus short and thick (Fig. 156) ..... *bipunctata*
3. Embolus long and thin (Fig. 123). Western United States (Map 17) ..... *grandis*
4. Radix with a distinct ectal lobe below tip (Figs. 130-132, 135, 137, 139, 141) 5
4. Radix with no lobe near tip 6
5. California coast range south to Riverside County (Map 17) .... *atascadera*
5. Southern California (Map 17) ..... *palomara*
6. Radix with tip pointing ectally, above a notch, (Figs. 130-132) Southern California (Map 17) ..... *palomara*
6. End of radix pointing ectal but without notch below (Figs. 125, 146) 7
7. Base of embolus almost circular with rim curved outward (Figs. 144, 147) Western United States, southern British Columbia (Map 19) ..... *hespera*
7. Base of embolus oval with rim not curved outward (Fig. 128) Western United States and Mexico (Map 17) ..... *mexicana*

Steatoda bipunctata (Linnaeus)

Figures 86-89, 155-156; Map 16.

Aranea bipunctata Linnaeus, 1758, Systema Naturae, 10th ed., p. 620.

Aranea 4-punctata, Fabricius, 1775, Systema Entomologiae, p. 434.

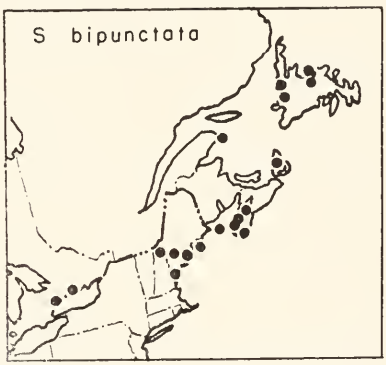
Aranea punctata, De Geer, 1778, Mémoires pour servir à l'histoire des Insectes, vol. 7, p. 255, pl. 15, fig. 1.

Theridion 4-punctatum, Walckenaer, 1805, Tableau des Aranéides, p. 73, pl. 7, figs. 69, 70.

Steatoda 4-punctatum, Sundevall, 1833, Conspectus Arachnidum, p. 17.
Phrurolithus ornatus C.L. Koch, 1839, Die Arachniden, vol. 6, p. 114, fig. 515.
Eucharia bipunctata, C.L. Koch, 1845, *ibid.*, vol. 12, p. 99, fig. 1027.
Theridium cruciatum Giebel, 1869, Zeitschr. Ges. Naturwiss., vol. 34, p. 303.
Steatoda bipunctata, Thorell, 1856, Nova Acta reg. Soc. sci. Upsaliensis, ser. 3, vol. 2, p. 140. Keyserling, 1884, Die Spinnen Amerikas, vol. 2, pt. 1, p. 116, pl. 6, fig. 76, ♀, ♂. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 187. Wiehle, 1937, *in* Dahl, Die Tierwelt Deutschlands, pt. 33, p. 193, figs. 200-204, ♀, ♂. Kurata, 1939, Canadian Ent., vol. 53, p. 81. Roewer, 1942, Katalog der Araneae, vol. 1, p. 412. Gertsch, 1946, in Procter, Biological Survey of the Mount Desert Region, pt. 7; Gertsch, 1949, American spiders, p. 258. Locket and Millidge, 1953, British spiders, vol. 2, p. 56, figs. 38, ♀, ♂. Hackman, 1954, Acta Zool. Fennica, vol. 79, p. 4.

Types. The type locality is presumably Sweden.

Diagnosis. This species may have the legs very slightly shorter



Map 16. American distribution of *Steatoda bipunctata* (Linnaeus).

than in other species of *Steatoda*. It is readily distinguished by comparison of the genitalia (Figs. 89, 155, 156). The total length of females is 4.8-7.3 mm., of males, 4.4-6.0 mm.

Natural History. This species may have been introduced in recent times. It seems to have survived mainly along the coast or the shores of Lake Ontario. C. Dondale has collected specimens on a barn.

Distribution. Europe, Siberia, Kamchatka (Wiehle, 1937). Introduced in French Guiana and Venezuela (Keyserling, 1884).

Probably introduced on the coast of Maine to Newfoundland, north shore of Lake Ontario (Map 16).

Records. Newfoundland: (Hackman, 1954); Nicholsville. *Nova Scotia:* Weymouth; Grand Pré; Baddeck; Barrington; Lequille. *New Brunswick:* Grand Manan Isl. *Quebec:* Bonaventura Isl. *Ontario:* Toronto (W. J. Gertsch); Lakeport. *Maine:* Cumberland Co.: Sebago Lake; Hancock Co.: Mt. Desert Isl.; Lincoln Co.: Jefferson; York Co.: Saco. *New Hampshire:* Coos Co.: Gorham, 1946, (E. L. Bell).

Steatoda grandis Banks

Figures 92-97, 119-123; Map 17.

Steatoda grandis Banks, 1901, Proc. Acad. Nat. Sci. Philadelphia, p. 578; 1910, Bull. U.S. Natl. Mus., no. 72, p. 21, Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 188. Roewer, 1942, Katalog der Araneae, vol. 1, p. 413.

Steatoda zionis Chamberlin and Ivie, 1935, Bull. Univ. Utah, biol. ser. vol. 2, no. 8, p. 12, figs. 36, 42, ♀, ♂. Roewer, 1942, Katalog der Araneae, vol. 1, p. 414. NEW SYNONYMY.

Steatoda merula L. Fox 1940, Proc. Biol. Soc. Washington, vol. 53, p. 41, fig. 3, ♀. NEW SYNONYMY.

Types. Female type of *S. grandis* from Albuquerque, New Mexico, in the Museum of Comparative Zoology. Male holotype, female allotype of *S. zionis* from Zion National Park, Utah, in the American Museum of Natural History. Female type of *S. merula* from Mt. Lemmon, Arizona, in the United States National Museum (no. 1368).

Diagnosis and Variation. The epigyna of this species are extremely variable, particularly in the southern portion of its range (Figs. 93-97). The epigynum of the type of *S. grandis* resembles Figure 93. Only in the narrower septum and slightly deeper depression on each side of the epigynum does this species differ from *S. americana;* furthermore the depression of the epigynum is frequently filled with a material difficult or impossible to remove. The epigyna of the types of both *S. grandis* and *S. merula* are partly filled in this way. The palpus, in contrast to the female genitalia, shows little variation (Figs. 119, 120, 123). Only two males from central Colorado had the tip of the radix slightly different (Figs. 121, 122). Total length of females 4.9-9.0 mm.; that of males 4.3-7.4 mm.

Natural History. In Colorado this species has been collected under stones, rocks and in cliffs from lower elevations (7000-8000 ft.) than *S. hespera.*

Distribution. Western United States (Map 17).

Records. South Dakota: Custer Co.: Blue Bell, 4900 ft., ♀. Pennington Co.: Horsethief Lk., ♀ ; S. of Rapid City, ♀. *Wyoming:* Devil's Tower Natl. Mon., Aug. 5, 1952 (B. Malkin), ♀.

Map 17. Distribution of *Steatoda grandis* Banks, *S. palomara* Chamberlin and Ivie and *S. atascadera* Chamberlin and Ivie.

Colorado: Archuleta Co.: Piedra, ♀. Boulder, ♀. Denver, ♀. Douglas Co.: Parker, ♀. El Paso Co.: Cascade, ♀. Gunnison Co.: Taylor River, ♀. La Plata Co.: Durango, ♀. Larimer Co.: Estes Park, 7800 ft., ♂ ; Fort Collins, ♀. Mineral Co.: West Fork of Wolf Creek, 7800 ft., ♀. Rio Grande Co.: Monte Vista, ♀. Routt Co.: Steamboat Springs, ♀. Teller Co.: Pikes Peak, 10,000 ft., ♀. *New Mexico:* Colfax Co.: Raton, ♂. Bernalillo Co.: Sandia Mts., ♀. Catron Co.: 25 mi. N. of Alma, ♀.

Lincoln Co., ♀. Santa Fe Co.: 10 mi. S. of Santa Fe; Little Tesugue Canyon, ♂. Valencia Co.: Bluewater. *Utah:* Carbon Co.: Helper, ♀; Price, ♀, ♂. Iron Co.: Parowan, ♀ ♂. Emery Co.: Ferron, ♀, ♂. Garfield Co.: Escalante, ♂; Red Canyon, ♀, ♂. Millard Co.: Scipio, ♀. San Juan Co.: Monticello, ♀. Sevier Co.: Fish Lk., ♀; Richfield, ♀, ♂. Uintah Co.: Vernal, ♀; Watson, ♀; White Riv. nr. Evacuation Cr., 5000 ft., ♀. Utah Co.: Levan, ♀. Wayne Co.: Fruita, ♀; Notom, ♀, ♂. *Arizona:* Apache Co.: Wide Ruin, ♀, ♂; 17 mi. NE. of Whiteriver, ♀, ♂; Hannagan, ♀. Cochise Co.: Chiricahua Mts. (many collections) ♀, ♂; Carr Canyon, Huachuca Mts., ♀. Coconino Co.: Oak Cr. Canyon, ♀. Gila Co.: 7 mi. N. of Payson, ♀; Middle Pioneer Cr., Pinal Mts., ♀, ♂. Graham Co.: Graham Mt. (many collections) ♀, ♂. Pima Co.: Santa Catalina Mts. (many collections) ♀, ♂. Santa Cruz Co.: Santa Rita Mts. (many collections), ♀, ♂. Yavapai Co.: Prescott, ♀. *Oregon:* Wheeler Co.: Richmond, Fall 1948 (Donnely), ♀; 3 Aug. 1951 (V. Roth), ♀, ♂.

Steatoda mexicana, new name

Figures 98-103, 124-128; Map 18.

Stearodea americana F.O.P. Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 377, pl. 35, fig. 12, ♀. Not *Steatoda americana* (Emerton).

Steatoda americana, Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 187. Roewer, 1942, Katalog der Araneae, vol. 1, p. 413. Not *Steatoda americana* (Emerton). Not Banks, 1909, Proc. Acad. Nat. Sci., Philadelphia, vol. 61, p. 205.

Steatoda grandis, Chamberlin and Ivie, 1935, Bull. Univ. Utah, biol. ser., vol. 2, no. 8, figs. 37, 40, 41, ♀, ♂. Not *S. grandis* Banks.

Types. Two female syntypes from Omiltemi, Guerrero in the British Museum (Natural History).

Diagnosis and Variation. The epigyna of this species are very variable particularly in the northern and eastern portion of its range (Figs. 99-103). The epigynum of a syntype examined resembles that from St. George, Utah (Fig. 99) but the scape is slightly wider. However, it is slightly narrower than that from Chiricahua Mountains (Fig. 103). Most females can readily be told from *S. grandis* by the wider scape of the epigy-

num. The shape of the radix of the palpus is variable. Some almost resemble that of *S. grandis*, in others the radix is long and stretched. The shape of the base of the embolus (Fig. 128) readily distinguishes this species from *S. hespera*. Total length of females 5.1-9.0 mm.; of males 4.8-5.7 mm.

Distribution. Idaho to Texas, Arizona south to Guerrero (Map 18).

Records. Texas: Big Bend Natl. Pk., Chisos Mts., ♀. Walker Co.: Huntsville, 2 Oct. 1950 (M. A. Cazier), ♀. *Colorado:* Larimer Co.: Red Feather Lakes, June 14, 1933 (A. B. Klots) ♀. *New Mexico:* Otero Co.: Camp Mary White, ♀, ♂. *Idaho:* Bear Lake Co.: Bloomington, ♀, ♂. *Utah:* Bryce Canyon Natl. Pk., ♀; Garfield Co.; 15 mi. N. of Boulder, ♀; Henry Mts., ♀; 10 mi. SE.

Map 18. Distribution of *Steatoda mexicana*, new name.

of Panguitch, ♀. Salt Lake City, ♀. Sevier Co.: Fish Lk., ♀. Utah Co.: Lehi, ♀; west shore of Utah Lk., ♀, ♂. Washington Co.: St. George, ♀; Beaver Dam Wash., ♀. *Arizona:* Cochise Co.: Rustler's Camp. Chiricahua Mts., ♀, ♂. Coconino Co.: Flagstaff, ♀. Grand Canyon Natl. Pk., ♀. Graham Co.: Graham Mt., Pinecrest, ♀, ♂. Santa Cruz Co.: 4 mi. SE. of Ruby, ♀.

Yavapai Co.: Prescott, ♀. *Chihuahua:* SW. of Santa Barbara. 8400 ft., ♀. *Durango:* "Providencia," 7700 ft., ♀.

Steatoda palomara Chamberlin and Ivie

Figures 104, 105, 129-133; Map 17.

Steatoda palomara Chamberlin and Ivie, 1935, Bull. Univ. Utah, biol. ser., vol. 2, no. 8, p. 13, fig. 43, ♀. Roewer, 1942, Katalog der Araneae, vol. 1, p. 414.

Type. Female type from Mt. Palomar, California in the American Museum of Natural History.

Diagnosis. The epigynum (Fig. 105) and the tip of the radix of the palpus (Figs. 130-132) distinguish this species. Total length of females 5.0-6.8 mm.; males, 5.3 mm.

Distribution. Known only from San Diego County, California (Map 17).

Records. California: San Diego Co.: Mt. Palomar, July 25, 1931 (W. Ivie), ♀; July 13, 1953 (W. J. and J. W. Gertsch), ♀; 3000-5000 ft., June 30, 1956 (W. J. Gertsch and V. Roth), ♀, ♂; Descanso, June 25, 1947 (W. M. Pearce).

Steatoda atascadera Chamberlin and Ivie

Figures 106-109, 134-141; Map 17.

Steatoda atascadera Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., vol. 7, no. 1, p. 39, figs. 83, 84, ♀, ♂.

Types. Male holotype, female allotype from Atascadero Lake, San Luis Obispo County, California, from under concrete bridge at south end of lake, in the American Museum of Natural History.

Diagnosis and Variation. The epigyna (Figs. 107-109) and palpi (Figs. 134-141) of this species are extremely variable. Hardly two look alike. The tip of the radix of the male palp as well as the width of the anterior raised lobe of the epigynum separate this species from *S. palomara* and *S. hespera.* Total length of females 4.8-6.0 mm., of males, 3.8-4.4 mm.

Distribution. Coast range of California from Santa Cruz to Riverside County (Map 17).

Records. California: Los Angeles Co.: nr. Claremont; (V. Roth, W. J. Gertsch), ♀. San Gabriel Mts. (many records),

♀, ♂ ; Santa Monica Mts. (R. X. Schick), ♀. Glendale (E. I. Schlinger), ♀. Monterey Co.: Hastings Nat. Hist. Reserve (J. Linsdale), ♂. Orange Co.: Silverado Canyon, Santa Ana Mts. (R. X. Schick) ♀. Riverside Co.: San Jacinto Mts. (R. X. Schick), ♀. Santa Cruz Co.: Big Trees Park (A. F. Archer), ♂ : Brookdale (W. H. Irvin), ♂. Yolo Co.: Davis (E. I. Schlinger). ♀.

Steatoda hespera Chamberlin and Ivie

Figures 90, 91, 110-115, 142-147; Map 19.

Steatoda hespera Chamberlin and Ivie, 1933, Bull. Univ. Utah, biol. ser., vol. 2, no. 2, p. 9, figs. 4-6, ♀, ♂. Gertsch, 1939, Amer. Mus. Novitates, no. 1032, p. 4. Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., vol. 6, no. 3, p. 12. Roewer, 1942, Katalog der Araneae vol. 1, p. 414. Levi and Levi, 1951, Zoologica, vol. 36, p. 220; 1955, Canadian Field Nat., vol. 69, p. 69. Lowrie and Gertsch, 1955, Amer. Mus. Novitates, no. 1736, p. 7.

Types. Syntypes from Clear Creek, Raft River Mountains, Utah, in the American Museum of Natural History.

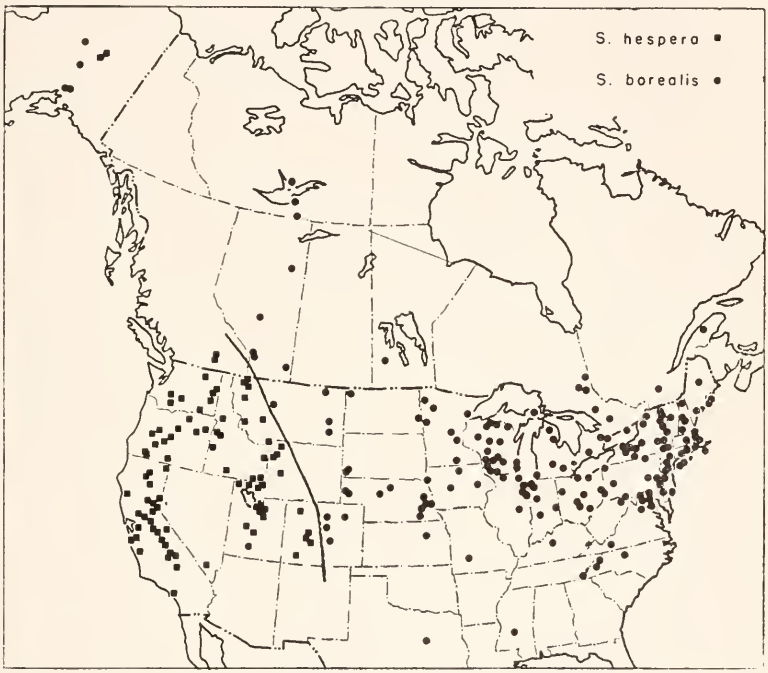
Diagnosis and Variation. The proportions of the anterior raised lobe as well as the even width of the depressed area of the epigynum (Figs. 111-115) distinguish this species from *S. borealis* and *S. atascadera.* The radix of the palpus lacks the median lobe typical of *S. borealis* and lacks the lobe below the tip typical of *S. atascadera* (Figs. 143, 146). Specimens from the western part of the range seem slightly larger in size than those of the east. Total length of females 4.2-7.5 mm.; of males, 3.6-5.4 mm.

Natural History. In Colorado this species has been collected under bark of dead conifers and in cabins at elevations between 8500 ft. and timberline.

Distribution. Western United States (Map 19).

Records. British Columbia: Salmon Arm; Vernon. *Montana:* Helena; Flathead Co.; Gallatin Co.; Glacier Natl. Pk.; Ravalli Co. *Wyoming:* Grand Teton Natl. Pk.; Sublette Co.; Teton Co.; Yellowstone Natl. Pk. *Colorado:* Gunnison Co.; La Plata Co.; Pitkin Co.; Routt Co. *Idaho:* Adams Co.; Bear Lake Co.: Franklin Co.; Idaho Co.; Payette Co.; Teton Co.; Twin Falls Co.;

Valley Co. *Utah:* Box Elder Co.; Cache Co.; Garfield Co.; Millard Co.; Rich Co.; Salt Lake Co.; Sevier Co.; Summit Co.; Utah Co.; Wasatch Co. *Nevada:* Clark Co.; Reno. *Washington:* Ferry Co.; Mt. Ranier Natl. Pk.; Spokane Co.; Walla Walla; Whitman Co.; Yakima. *Oregon:* Baker Co.; Crater Lk. Natl. Pk.; Deschutes Co.; Grant Co.; Jackson Co.; Klamath Co.; Lake Co.; Lane Co.; Morrow Co.; Three Sisters Primitive Area;



Map. 19. Distribution of *Steatoda hespera* Chamberlin and Ivie and *S. borealis* (Hentz).

Wheeler Co. *California:* Calaveras Co.; Contra Costa Co.; Eldorado Co.; Fresno Co.; Kings Canyon Natl. Pk.; Los Angeles Co.; Madera Co.; Mariposa Co.; Mendocino Co.; Modoc Co.; Mono Co.; Monterey Co.; Nevada Co.; Placer Co.; Sacramento Co.; Santa Clara Co.; Santa Cruz Co.; Sequoia Natl. Pk.; Shasta Co.; Sierra Co.; Siskiyou Co.; Tulare Co.; Yolo Co.; Yosemite Natl. Pk.; Yuba Co.

Steatoda borealis (Hentz)

Figures 116-118, 148-154; Map 19.

Theridion boreale Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 274, pl. 9, fig. 4, ♂; 1875, Spiders of the United States, p. 145, pl. 16, fig. 4, ♂ pl. 21, fig. 13, ♂.

Steatoda borealis, Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 19, pl. 4, fig. 1, ♀, ♂. Keyserling, 1884. Die Spinnen Amerikas, vol. 2, no. 1, p. 119, pl. 6, fig. 77, ♀, ♂. McCook, 1890, American Spiders, vol. 2, p. 55. Marx, 1890, Proc. U.S. Natl. Mus., vol. 12, p. 521; 1892, Proc. Ent. Soc. Washington, vol. 2, p. 156. Fox, W., *op. cit.*, p. 268. Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia, p. 31. Emerton, 1894, Trans. Connecticut Acad. Sci., vol. 9, p. 406. Baker, 1894, Ent. News, vol. 5, p. 164. Banks, 1895a, Jour. New York Ent. Soc., vol. 3, p. 84; 1895b, Ent. News, vol. 6, p. 182; 1899, Proc. Ent. Soc. Washington, vol. 4, p. 189. Emerton, 1902, The common spiders, p. 119, figs. 276-279, ♀, ♂. Scheffer, 1905, Trans. Kansas Acad. Sci., vol. 19, p. 192. Banks, 1907, Ann. Rept. Indiana Dept. Geol. and Nat. Res. no. 31, p. 739. Bryant, 1908, Occas. Papers Boston Soc. Nat. Hist., no. 9, p. 16. Banks, 1910, Bull. U.S. Natl. Mus., no. 72, p. 21. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 188. Banks, 1911, Proc. Acad. Nat. Sci. Philadelphia, vol. 63, p. 445. Comstock, 1912, The spider book, p. 360, fig. 363, ♀. Emerton, 1913, Appalachia, vol. 12, p. 155. Barrows, 1918, Ohio Jour. Sci., vol. 18, p. 304. Bishop, 1924, Bull. New York State Mus. no. 251, p. 21. Barrows, 1925, Ann. Ent. Soc. Amer., vol. 18, p. 506. Emerton, 1928, Univ. Toronto Studies, Biol., vol. 32, p. 45. Crosby and Bishop, 1928, Mem. Cornell Univ. Agr. Exp. Sta., no. 101, p. 1040. Emerton, 1930, Publ. Nantucket Maria Mitchell Assoc., vol. 3, p. 164. Worley, 1931, Studies Univ. Nebraska, vol. 27, p. 28. Chickering, 1931, Papers Michigan Acad. Sci., vol. 15, p. 351. Elliott, 1932, Proc. Indiana Acad. Sci., vol. 41, p. 424. Chamberlin and Ivie, 1933, Bull. Univ. Utah, biol. ser., vol. 2, no. 2, fig. 7, ♀. Stiles and Detwiler, 1938, Proc. Iowa Acad. Sci., vol. 45, p. 286. Kurata, 1939. Canadian Nat., vol. 53, p. 81. Comstock, 1940, The spider book, rev. ed. p. 375; fig. 363, ♀. Kurata, 1941, Univ. Toronto Studies, biol. ser., no. 48, p. 109. Truman, 1942, Bull. Univ. Pittsburgh, vol. 38, no. 2, p. 4. Roewer, 1942, Katalog der Araneae, vol. 1, p. 413. Lowrie, 1942, Bull. Chicago Acad. Sci., vol. 6, p. 169. Kurata, 1943, Canadian Ent., vol. 57, p. 10. Muma, 1943, Common spiders of Maryland, p. 65, pl. 4, fig. 2, pl. 12, fig. 20. Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 46. Muma, 1945, Bull. Agr. Exp. Sta. Univ. Maryland, no. A38, p. 27. Gertsch, 1946, in Procter, Biol. Surv. of the Mount Desert Reg., pt. 7, p. 519. Rapp, 1946, Bull. Brooklyn Ent. Soc., vol.

41, p. 4. Chamberlin and Ivie, 1947, Bull. Univ. Utah, biol. ser., vol. 10, no. 3, p. 27. Lowrie, 1948, Ecology, vol. 29, p. 350. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 85, figs. 51-56, 2014, ♀, ♂. Gertsch, 1949, American spiders, p. 258. Kurata, 1949, Canadian Ent., vol. 81, p. 127. Elliott, 1953, Proc. Indiana Acad. Sci., vol. 62, p. 309. Kaston, 1953, How to know the spiders; p. 162. Levi and Field, 1954, Amer. Midland Nat., vol. 51, p. 444. Kaston, 1955, Trans. Illinois Acad. Sci., vol. 47, p. 166.

Type locality. "United States." The type specimens are lost.

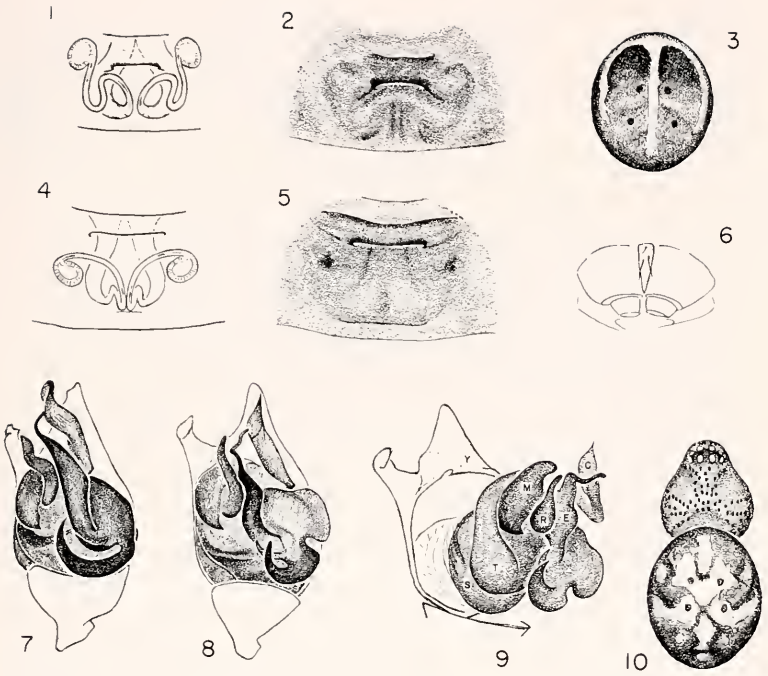
Diagnosis. The wide raised median lobe, the swollen posterior area of the depression of the epigynum (Figs. 117-118), and the median lobe on the palpal radix (Fig. 148) distinguish this species from *S. hespera.* Total length of females: 3.8-7.0 mm.; of males, 4.3-5.9 mm.

Natural History. This is the common *Steatoda* of the eastern United States, which is found on buildings.

Distribution. East of the Rocky Mountains south to Texas and North Carolina; north to Alaska (Map 19). There are more old records from the southern states than recent ones. Shreveport, Louisiana (Banks, 1899), Alabama (Hentz, 1875) and Georgia (Keyserling, 1884), however, this species has only rarely been collected in these states during the last fifty years. One record probably an accidental one, is that of a male and female collected at Lakeside, San Diego County, California, by N. Banks, another from Eugene, Oregon, April 1947 (B. Malkin). ♂, probably introduced.

Records. Alaska: (Chamberlin and Ivie, 1947); Fox; Tanana; Mt. McKinley Natl. Pk. *Nova Scotia:* Coldbrook. *Quebec:* Montreal; Matapédia. *Ontario:* (Emerton, 1928; Kurata, 1939, 1941, 1943); 36 mi. N. of North Bay; St. Thomas; Lake Temagami; Newmarket; Haliburton. *Manitoba:* Riding Mountain. *Northwest Territory:* (Kurata, 1949), Outpost Island, Great Slave Lk. *Alberta:* Medicine Hat; MacMurray; Seba Beach; Mt. Sentinel. *Maine:* (Bishop, 1924); Cumberland Co.; Piscataquis Co. *New Hampshire:* Carroll Co.; Cheshire Co.; Coos Co.; Grafton Co. *Vermont:* Addison Co. *Massachusetts:* (Emerton, 1930); Essex Co.; Middlesex Co.; Norfolk Co.; Plymouth Co.; Worcester Co. *Rhode Island:* Providence. *Connecticut:* (Kaston, 1948). *New York:* (Banks, 1892; Bishop and Crosby, 1928); Clinton Co.; Fulton Co.; Jefferson Co.; Nassau Co.; Rockland

Co.; St. Lawrence Co.; Steuben Co. *New Jersey:* (Rapp. 1946); Bergen Co.; Cape May Co.; Mercer Co.; Morris Co. *Pennsylvania:* Bradford Co.; Montgomery Co.; Philadelphia Co.; Pittsburgh; Schuykill Co. *Delaware:* Wilmington. *Maryland:* (Muma, 1943, 1945). *Virginia:* Fairfax Co.; Pulaski Co. *West Virginia:* Ohio Co. *North Carolina:* (Banks, 1911); Avery Co.; Buncombe Co.; Guilford Co.; Swaine Co. *Mississippi:* Rankin Co. *Ohio:* Athens Co.; Columbiana Co.; Cuyahoga Co. *Michigan:* (Hentz, 1875; Baker, 1894; Chickering, 1931; Lowrie, 1948); Chippewa Co.; Ogemaw Co.; Washtenaw Co. *Indiana:* (Banks, 1907; Lowrie, 1948; Elliott, 1953). *Kentucky:* Hardin Co. *Wisconsin:* (Levi and Field, 1954); Crawford Co.; Grant Co.; Marathon Co.; Milwaukee Co.; Racine Co. *Illinois:* (Lowrie, 1948, Kaston, 1955); Champaign Co.; Cook Co.; Winnebago Co. *Minnesota:* Clay Co.; Clearwater Co.; Freeborn Co.; Marshall Co.; Mille Lacs Co.; Minneapolis; Saint Louis Co. *Iowa:* (Stiles and Detwiler, 1938); Ames; Cerro Gordo Co.; Woodbury Co. *Missouri:* (Banks, 1895b). *North Dakota:* Divide Co.; Cass Co. *South Dakota:* Custer Co. *Nebraska:* (Worley, 1931); Saline Co. *Kansas:* Riley Co. *Texas:* McLellan Co.: Moody, Sept. 1941 (C. and M. Goodnight), ♀. *Montana:* Cascade Co.; Custer Co.; Daniel Co.; Prairie Co. *Colorado:* Denver; El Paso Co.; Larimer Co.; Morgan Co.



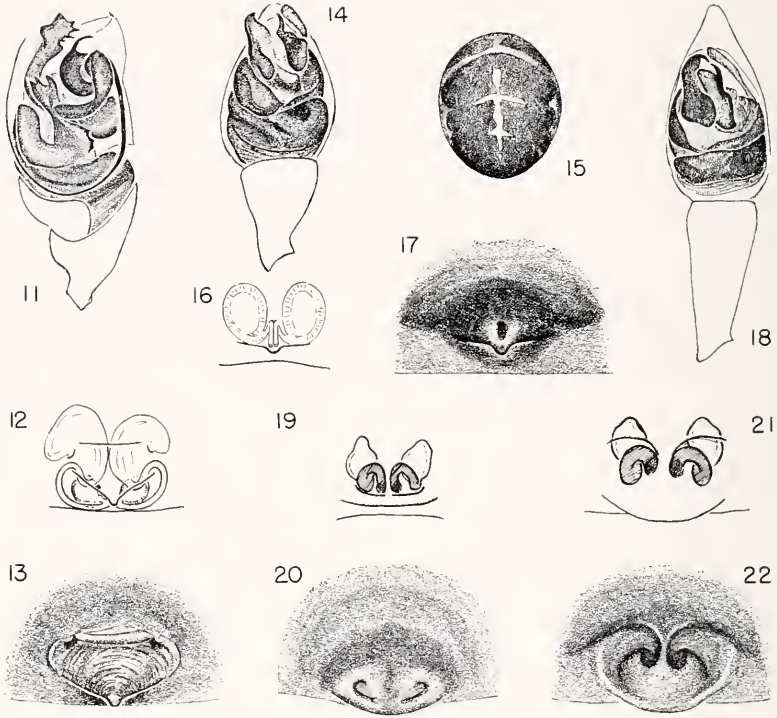
Figs. 1-3. *Crustulina sticta* (O.P. Cambridge). 1. Female genitalia, ventral view. 2. Epigynum. 3. Abdomen of female, dorsal view.

Figs. 4-6. *C. altera* Gertsch and Archer. 4. Female genitalia, ventral view. 5. Epigynum. 6. Colulus and spinnerets.

Fig. 7. *C. sticta* (O.P. Cambridge), left palpus.

Figs. 8-10. *C. altera* Gertsch and Archer. 8. Palpus. 9. Palpus expanded, subventral view. 10. Female, dorsal view.

Abbreviations: C, conductor; E, embolus; M, median apophysis; R, radix; S, subtegulum; T, tegulum; Y, cymbium.



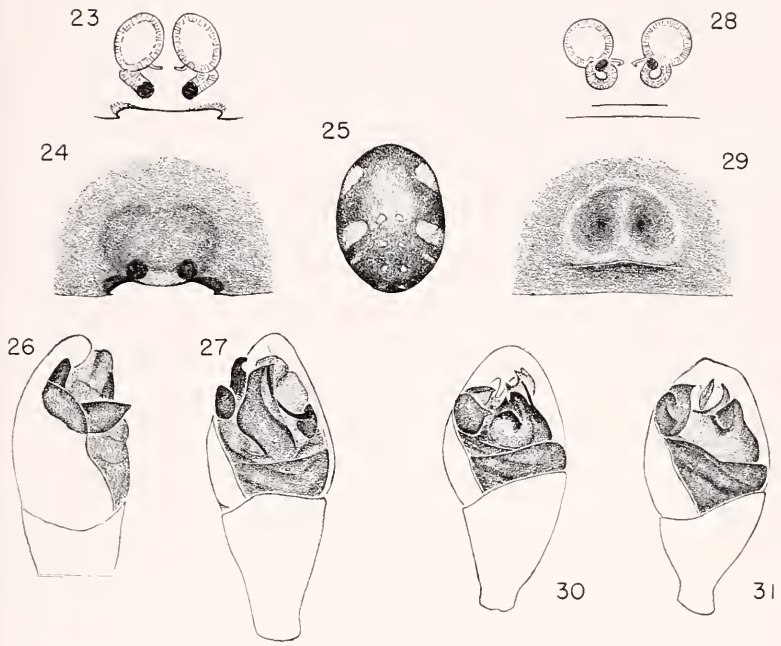
Figs. 11-13. *Steatoda nigrofemorata* (Keyserling). 11. Left palpus. 12. Female genitalia, ventral view. 13. Epigynum.

Fig. 14. *S. quaesita* (O.P. Cambridge), palpus.

Figs. 15-18. *S. moesta* (O.P. Cambridge). 15. Abdomen of female, dorsal view. 16. Female genitalia, ventral view. 17. Epigynum. 18. Palpus.

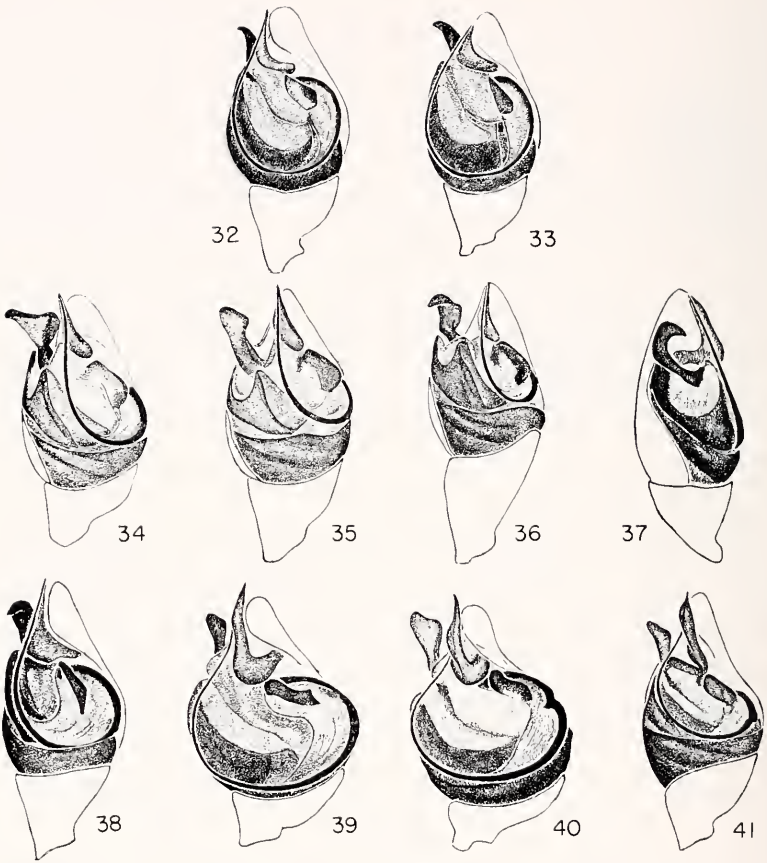
Figs. 19, 20. *S. saltensis*, new species. 19. Female genitalia, ventral view. 20. Epigynum.

Figs. 21, 22. *S. autumnalis* (Banks). 21. Female genitalia, ventral view. 22. Epigynum.



Figs. 23-27. *Steatoda transversa* (Banks). 23. Female genitalia, ventral view. 24. Epigynum. 25. Abdomen of female, dorsal view. 26, 27. left palpus. 26. Mesal view. 27. Ventral view.

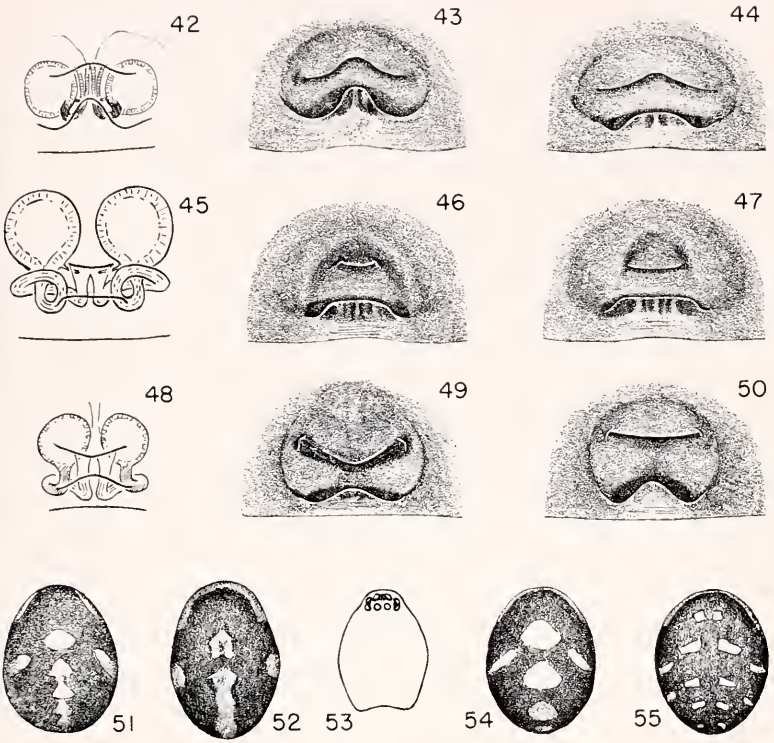
Figs. 28-31. *S. quadrimaculata* (O.P. Cambridge). 28. Female genitalia, ventral view. 29. Epigynum. 30, 31. Palpus. 30. (Tamaulipas). 31. (Guerrero).



Figs. 32, 33. *Steatoda fulva* (Keyserling), left palpus. 32. (California). 33. (Florida).

Figs. 34-36. *S. medialis* (Banks), palpus. 34. (Texas). 35. (Arizona). 36. (California).

Figs. 37-41. *S. pulcher* (Keyserling), palpus. 37. Mesal view (California. 38-41. Ventral view. 38. (California). 39. (Texas). 40. (Coahuila). 41. (Morelos).



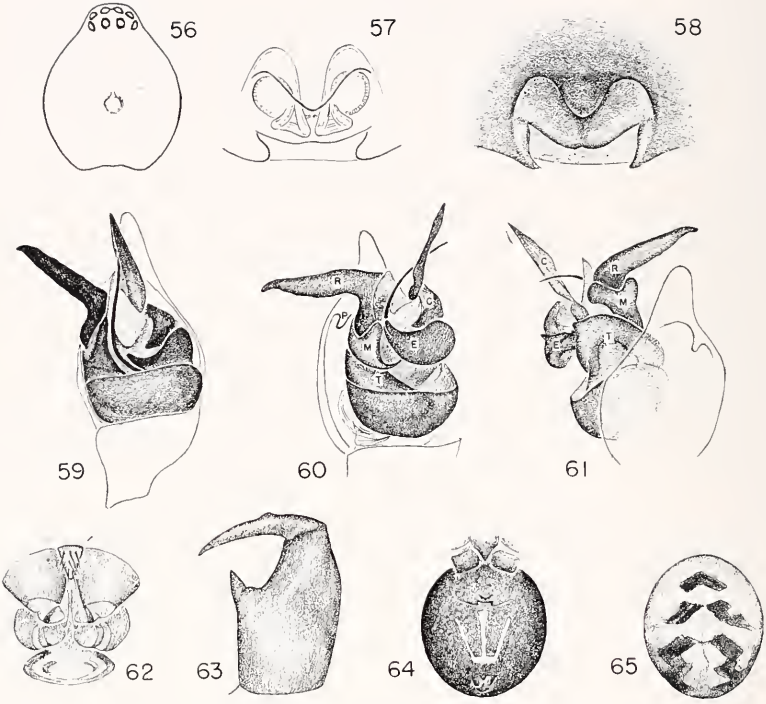
Figs. 42-44. *Steatoda medialis* (Banks). 42. Female genitalia, ventral view. 43, 44. Epigynum.

Figs. 45-47. *S. fulva* (Keyserling). 45. Female genitalia, ventral view. 46, 47. Epigynum.

Figs. 48-51. *S. pulcher* (Keyserling). 48. Female genitalia, ventral view. 49, 50. Epigynum. 51. Abdomen of a female, dorsal view.

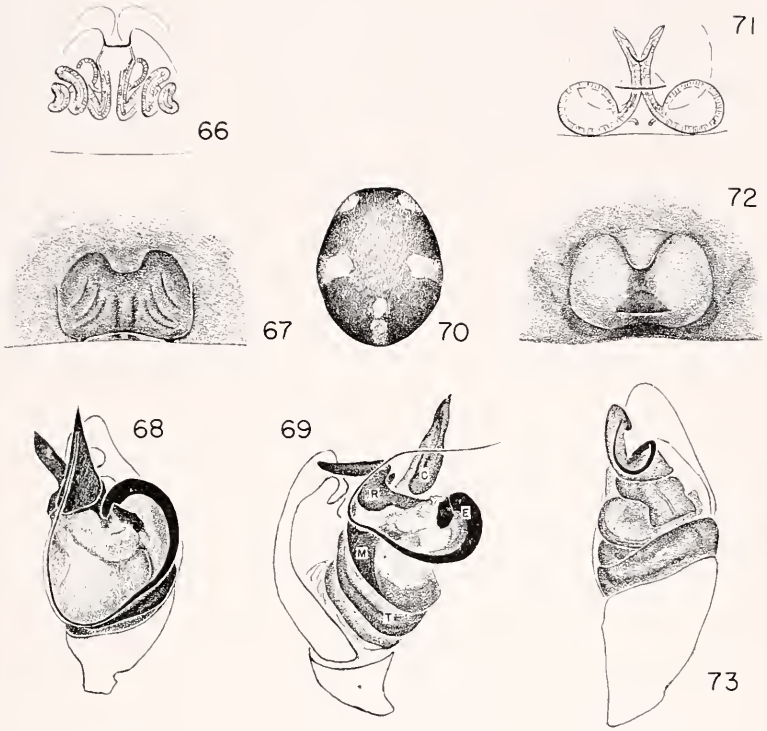
Fig. 52. *S. fulva* (Keyserling), abdomen of female, dorsal view.

Figs. 53-55. *S. medialis* (Banks). 53. Carapace of female. 54, 55. Abdomen of female, dorsal view.



Figs. 56-65. *Steatoda albomaculata* (De Geer). 56. Carapace of female. 57. Female genitalia, ventral view. 58. Epigynum. 59-61. Left palpus. 60. Expanded, subventral view. 61. Expanded, subcetal view. 62. Colulus and spinnerets. 63. Left chelicerae of male, inside view. 64-65. Abdomen of female. 64. Ventral view (Colorado). 65. Dorsal view (Massachusetts).

Abbreviations: C, conductor; E, embolus; M, median apophysis; P, paracymbial hook; R, radix; T, tegulum.



Figs. 66-69. *Steatoda americana* (Emerton). 66. Female genitalia, ventral view. 67. Epigynum. 68. Left Palpus. 69. Palpus, expanded, subventral view.

Figs. 70-73. *S. septemmaculata* (Keyserling). 70. Abdomen of female, dorsal view. 71. Female genitalia, ventral view. 72. Epigynum. 73. Palpus.

Abbreviations: C, conductor; E, embolus; M, median apophysis; R, radix; T, tegulum.

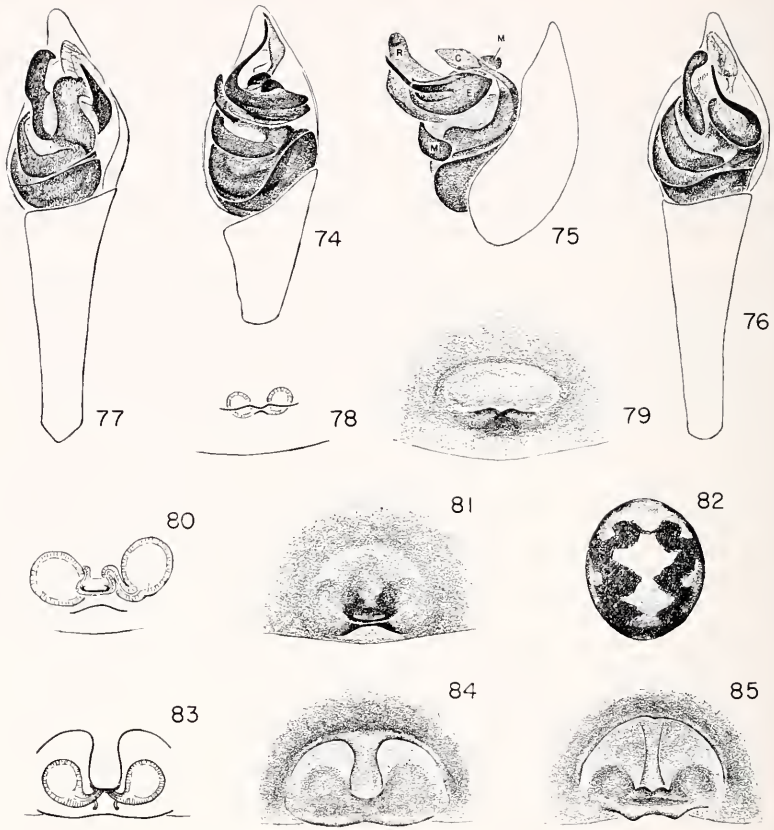


Fig. 74. *Steatoda grossa* (C.L. Koch), left palpus.

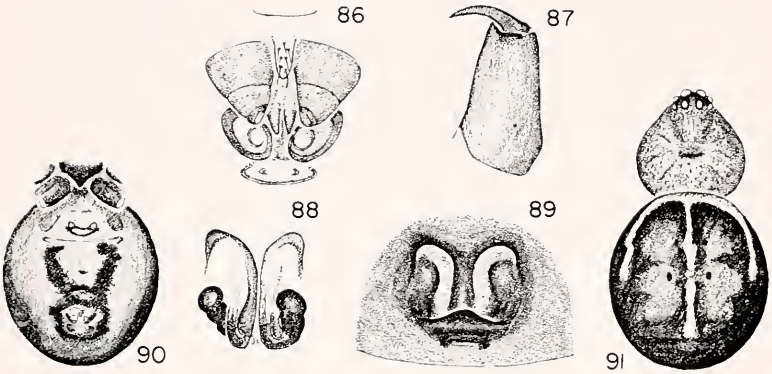
Figs. 75, 76. *S. triangulosa* (Walckenaer), palpus. 75. Expanded, ectal view. 76. Ventral view.

Figs. 77-79. *S. castanea* (Clerck). 77. Palpus. 78. Female genitalia ventral view. 79. Epigynum.

Figs. 80-82. *S. triangulosa* (Walckenaer). 80. Female genitalia, ventral view. 81. Epigynum. 82. Abdomen of female, dorsal view.

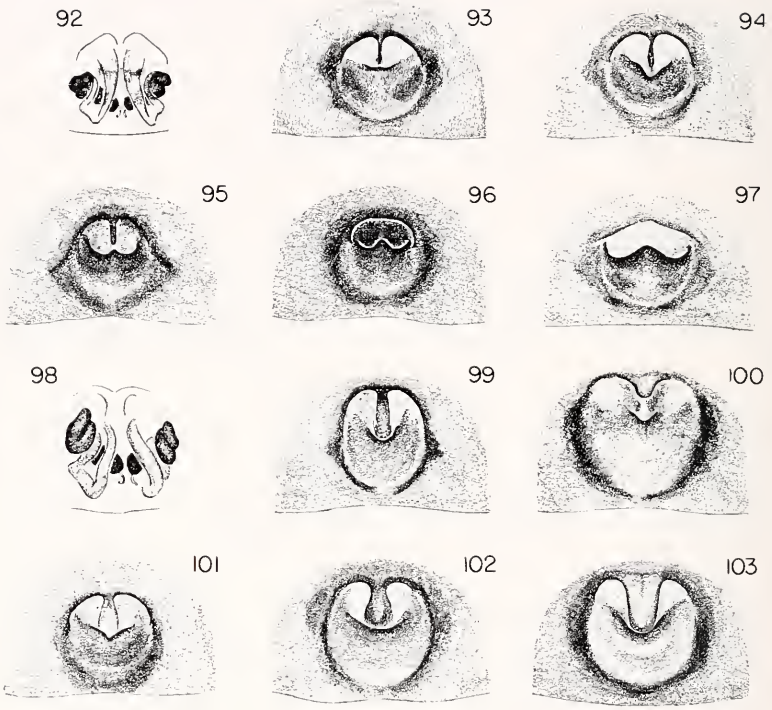
Figs. 83-85. *S. grossa* (C.L. Koch). 83. Female genitalia, ventral view. 84. Epigynum (California). 85. Epigynum (Michoacan).

Abbreviations: C, conductor; E, embolus; M, median apophysis; R, radix.



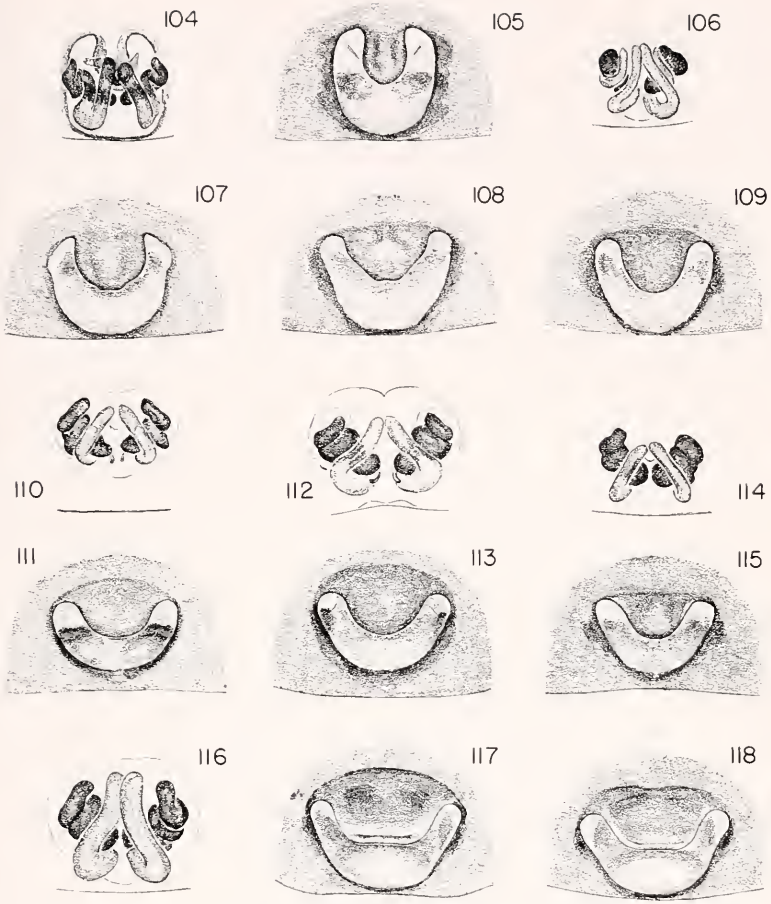
Figs. 86-89. *Steatoda bipunctata* (Linnaeus). 86. Colulus and spinnerets. 87. Left chelicera of female, inside view. 88. Female genitalia, dorsal view. 89. Epigynum.

Figs. 90, 91. *S. hespera* Chamberlin and Ivie, female. 90. Abdomen, ventral view. 91. Dorsal view.



Figs. 92-97. *Steatoda grandis* Banks. 92. Female genitalia, dorsal view (Zion Natl. Pk.). 93-97. Epigynum. 93. (Zion Natl. Pk.). 94. (Richfield, Utah). 95. (Graham Mts., Arizona). 96, (Hannagan, Arizona). 97. (Alma, New Mexico).

Figs. 98-103. *S. mexicana,* new name. 98. Female genitalia, dorsal view (Chiricahua Mts., Arizona). 99-103. Epigynum. 99. (St. George, Utah). 100. (Big Bend, Texas). 101. (Otero Co., New Mexico). 102. (Utah Lk., Utah). 103. (Chiricahua Mts., Arizona).

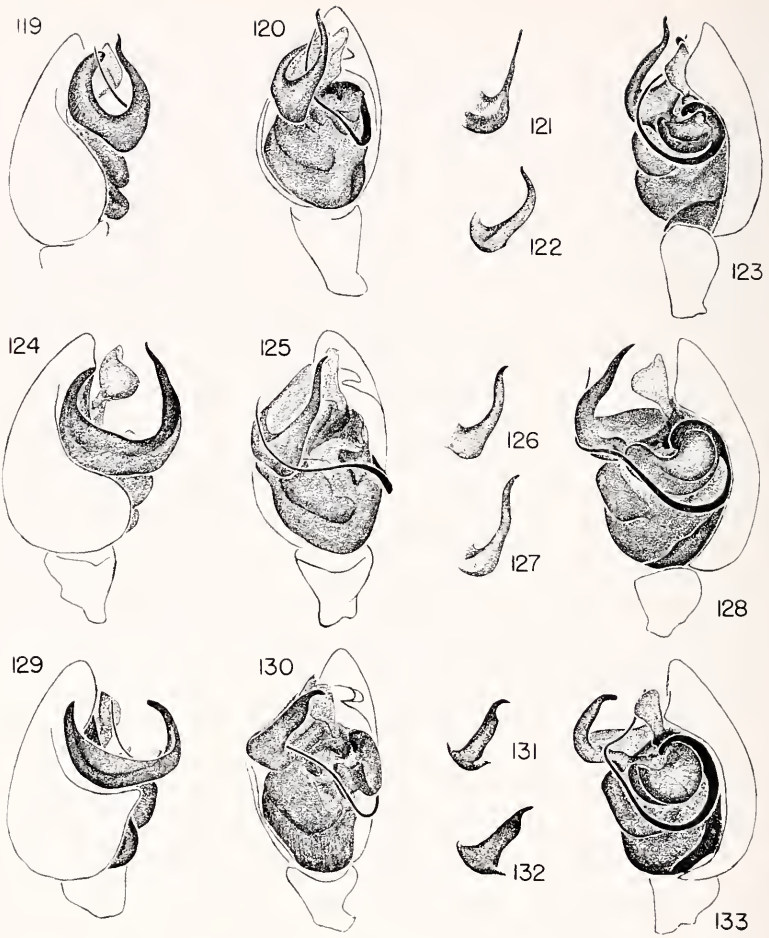


Figs. 104, 105. *Steatoda palomara* Chamberlin and Ivie. 104. Female genitalia, dorsal view. 105. Epigynum.

Figs. 106-109. *S. atascadera* Chamberlin and Ivie. 106. Female genitalia, dorsal view. 107-109. Epigynum (all from San Gabriel Mts.).

Figs. 110-115. *S. hespera* Chamberlin and Ivie. 110, 112, 114. Female genitalia, dorsal view. 111, 113, 115. Epigynum. 110, 111. (Montana). 112, 113. (Colorado). 114, 115. (California).

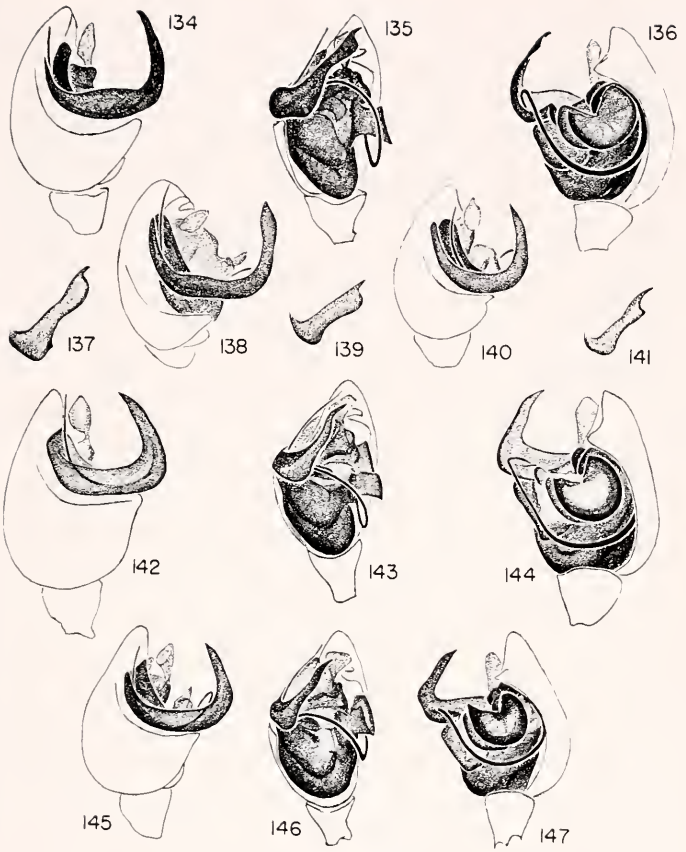
Figs 116-118. *S. borealis* (Hentz). 116. Female genitalia, dorsal view. 117, 118. Epigynum. 116, 117. (Wisconsin). 118. (North Carolina).



Figs. 119-123. *Steatoda grandis* Banks, left palpus. 119, 120, 123. (Zion Natl. Pk.). 119. Mesal view. 120. Ventral view. 121, 122. Radix, ventral view. 121. (Denver, Colorado). 122. (Estes Park, Colorado). 123. Ectal view.

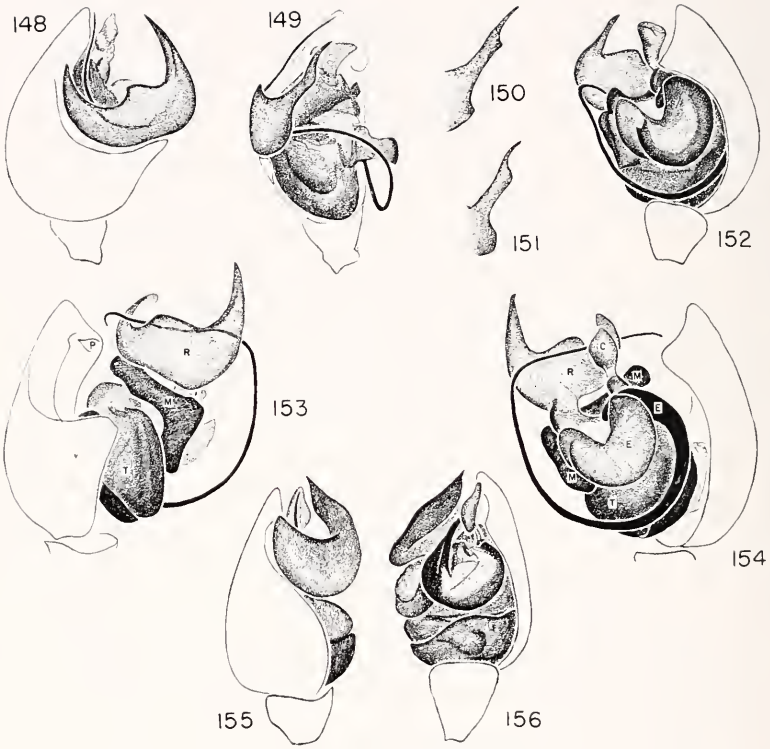
Figs. 124-128. *S. mexicana*, new name, palpus. 124, 125, 128. (Chiricahua Mts., Arizona). 124. Mesal view. 125. Ventral view. 126, 127. Radix, ventral view. 126. (Utah Lk., Utah), 127. (Bloomington, Idaho). 128. Mesal view.

Figs. 129-133. *S. palomara* Chamberlin and Ivie, palpus (all from Mt. Palomar, California). 129. Mesal view. 130. Ventral view. 131, 132. Radix of two different specimens. 133. Ectal view.



Figs. 134-141. *Steatoda atascadera* Chamberlin and Ivie, Left palpus. 134, 135, 136. (San Gabriel Mts., California). 134. Mesal view. 135. Ventral view. 136. Ectal view. 137. Radix, ventral view (Fish Canyon). 138, 139. (San Gabriel Mts.). 138. Mesal view. 140, 141. (Santa Cruz Co.). 140. Mesal view. 141. Radix, ventral view.

Figs. 142-147. *S. hespera* Chamberlin and Ivie, palpus. 142-144. (Montana). 145-147. (California). 142, 145. Mesal view. 143, 146. Ventral view. 144, 147. Ectal view.



Figs. 148-154. *Steatoda borealis* (Hentz), left palpus. 148, 149, 152. (Wisconsin). 148. Mesal view. 149. Ventral view. 152. Ectal view. 150, 151. Radix, ventral view. 150. (South Dakota). 151. (Massachusetts). 153, 154. Expanded. 153. Mesal view. 154. Ectal view.

Figs. 155-156. *S. bipunctata* (Linnaeus), palpus. 155. Mesal view. 156. Ectal view.

Abbreviations: C, conductor; E, embolus; M, median apophysis; P, paracymbial hook; R, radix; T, tegulum; Y, cymbium.

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 117, No. 4

CONTRIBUTION TO A REVISION OF THE EARTHWORM FAMILY OCNERODRILIDAE. THE GENUS *NEMATOGENIA*.

By G. E. Gates

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

September, 1957

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No.4 — *Contribution to a revision of the earthworm family Ocnerodrilidae.*
The genus NEMATOGENIA.

By G. E. GATES

INTRODUCTION

Since 1900, three supposedly endemic ocnerodrilids have been added to the long list (*cf.* Gates, 1942a) of North American species known only from types or original material. Three exotic species have been recorded (Gates, 1954, pp. 245-246) from the mainland or a neighboring island.

The casual spoil of other collecting (as so often in the past) now has made possible, for the first time in nearly six decades, some advance in our understanding of an important constituent of the oligochaete fauna of the continent.

The author's thanks are extended to Dr. P. J. Darlington, Jr., and to Dr. G. E. Pickford, for the opportunity of studying these interesting earthworms.

Genus NEMATOGENIA Eisen, 1900

Ocnerodrilus (*Nematogenia*) Eisen 1900, Proc. California Ac. Sci., (3) 2, p. 112. (Type species, *Pygmaeodrilus lacuum* Beddard, 1893.)
Nematogenia, Michaelsen, 1900, Das Tierreich, 10, p. 376.
Nematogenia, Stephenson, 1930, The Oligochaeta, p. 862.

The genus has been defined (Stephenson, 1930) essentially as follows: Dorsal pores present. Male pores, united with apertures of the single pair of prostates, on xvii. Spermathecae, adiverticulate, one pair, with pores on or behind 8/9. Gizzards, two, in vi-vii. Calciferous sacs, one pair, in ix. Metandric. Accordingly, two, three or four characters contraindicate inclusion of the Hispaniolan species, described below. Admission to all other ocnerodrilid genera is, by definition, also denied. Erection of at least two new genera is required by previous practice. Re-examination of the basis of classification of the family, however, first seems preferable.

Ocnerodrilid genera have been defined (cf. Stephenson, 1930, pp. 856-863) by the following characters; closeness of pairing

of setae, presence or absence of dorsal pores, presence or absence of ectal union of male deferent ducts with ducts of one pair of prostates, number of spermathecae and location of the spermathecal pores, number and location of gizzards, number and location of calciferous glands, presence or absence of diverticula on the spermathecal duct, number and location of prostates, andry (number and location of testes). However, little importance seems to have been attached to somatic structure. Calciferous glands and gizzards are not mentioned in the definition of *Pygmaeodrilus,* and species of *Gordiodrilus* may have a pair of lateral sacs or a single, median and ventral one, as well as one, two or no gizzards. Several genera have the same gizzard or calciferous-gland characters. Dorsal pores are present, in the Afro-American portion of the family (that with extramural calciferous glands), only in two species. Setal pairing is not mentioned in definitions of five of the genera recognized in 1930. Wide setal pairing, in anterior and middle regions of the body, has been reported from one species (Seychelles), in middle and posterior regions of the body, from two species (South America). Obviously, then, division of the family into genera has been based mainly on the genital organs.

The reproductive system, in all earthworm families, always has provided most of the characters for distinguishing and defining species. It is now being found that this system is "most susceptible to evolutionary change when reproduction is parthenogenetic" (Gates, 1956a, p. 227) for parthenogenesis permits more rapid accumulation of mutations. Such "evolutionary plasticity of the reproductive system necessitates considerable caution in use of its structures for taxonomic purposes at genus or higher level" (Gates, 1956b, p. 30).

Uniquely diagnostic somatic characters, in the Oligochaeta as known today, are very rare. None has been found in the Ocnerodrilidae. All species herein considered do, however, share a pair of somatic characters which are unknown in that combination elsewhere in the family. A combination of three genital characters, also found in each of the species herein considered is, however, shared with other groups that now have subgeneric or generic status. Obviously, then, since other characters are unavailable, the genus must be defined, at least primarily, by

somatic structure, as below. For the present, non-diagnostic but universally descriptive genital characters are retained in the definition. Latero-oesophageal hearts in x-xi appear to be characteristic in the family and need no mention.

Definition. Bithecal, pores at or behind 8/9. Biprostatic, pores on xvii. Male pores in or close to xvii.

Gizzards, two, in vi-vii. Calciferous glands, lateral, one pair, in ix. Spermathecae adiverticulate.

Distribution. Dominican Republic (Hispaniola).

The genus is known to be represented elsewhere only by a peregrine species formerly thought to be African but now apparently of American origin. This peregrine species extends the generic range to include the following: Panama, Costa Rica, Cameroons, Fernando Po, Belgian Congo, Ceylon.

Key to species of NEMATOGENIA

1. a. Body small, less than three mm thick, dorsal pores present 2
   b. Body larger, more than three mm thick, dorsal pores lacking. 3
2. a. Spermathecal pores on 8/9, male deferent and prostatic ducts of a side unite in parietes to open by a common pore. ..... *lacuum*
   b. Spermathecal pores midway between 8/9 and eq/ix, male pores discrete and behind prostatic pores. .... *panamaensis*
3. a. Typhlosole present 4
   b. Typhlosole lacking 5
4. a. Holandric ..... *alba*
   b. Metandric ..... *montana*
5. a. Intestinal origin in xii ..... *magna*
   b. Intestinal origin in xiv ..... *dominicana*

External characteristics that might provide a more useful key for preliminary identification are liable to individual variation. Until more is known about such differences, reliance on characters less liable to intraspecific variation is preferable. Deficiencies in our knowledge of species erected in the previous century complicate key construction and obviate any attempt to show phylogenetic relationships.

Nematogenia magna sp. nov.

Loma Rucilla, Cordillera Central, Dominican Republic, under grass in open pine woods at 8-10,000 feet, June 1938, 0-0-1. Dr. P. J. Darlington Jr. (Loma Rucilla is said to be the highest mountain in the West Indies.)

External characteristics. Length, 190 + mm (+ 70 mm?). Diameter, 8 mm. Segments, *ca.* 400 + (+ 129?). Pigmentation, unrecognizable (alcoholic preservation). Prostomium, prolobous. Secondary furrows; one well marked and postequatorial on each of iii-vii, one less distinct and pre-equatorial on each of v-vi, one pre-equatorial and one postequatorial deep furrow on each of viii-xiii. The posteriormost secondary annulus on each of ix-xi has a tertiary furrow. Nephropores and dorsal pores unrecognizable, the latter probably lacking.

Setae deeply retracted on preclitellar and clitellar segments, often unrecognizable, apparently small and not closely paired. Shortly behind the clitellum, $AB=CD<BC<AA$, $DD>\frac{1}{2}$C, but farther on $AB<CD<BC<AA$. Still more posteriorly AB ca.$=BC=$or slightly $<$ or slightly $>$ CD, AA appears to be consistently $>$ BC throughout though the difference may be small. In xvii, *a* setae probably present but *b* setae lacking.

Clitellum red (preservation artefact?), annular, on xiv-xxviii, the posteriormost portion of xiii with a slight red coloration.

Sphermathecal pores, one pair, at or slightly median to B, on 8/9. Female pores widely separated, equatorial, at approximate sites of apertures of *a* follicles, on xiv. Male and prostatic pores discrete, the former diagonally slit-like, the others smaller, circular and anterior, all at or just lateral to B and in a single, transverse, smooth, glistening area with distinct anterior and posterior boundaries about at levels of 16/17 and 17/18. Lateral margins of the area indistinct but in BC and nearer C. The pores of each side are in a slight depression within an area of special tumescence that is most obvious in AB.

No other genital markings.

Internal anatomy. Septum 6/7 slightly muscular, 7/8-10/11 thickly muscular, 11/12 strengthened but translucent.

Gizzards large, in vi and vii. Calciferous glands one pair, in ix, of solid type (no lumen), large, lateromesially flattened, thickly discoidal, slightly notched ventrally. Duct fairly thick,

soft, from pointed dorsal apex of each gland to lateral face of gut shortly in front of 9/10, with rather large aperture into gut lumen. Longitudinal lamellae on inner wall of gut in front of gland apertures gradually disappear anteriorly in ix. Intestinal origin in xii. Typhlosole lacking but at mD on roof of gut for some distance behind lvi there is a very low ridge, round to triangular in cross section. Supra-intestinal gland, in several segments around clv, an obvious yellowish thickening of gut roof where the tissues have a honey-comb texture.

Dorsal blood vessel single, disappearing from view within the pharyngeal glands in iii. Ventral trunk unrecognizable anterior to vii. Subneural lacking or unrecognizable, extra-oesophageals not distinguishable. Supra-oesophageal recognizable only in ix where a large branch on each side passes laterally on dorsal face of calciferous gland stalk and then down into the gland. Commissures of vi-ix obviously connect dorsal and ventral trunks. Commissures, or hearts, of x-xi probably latero-oesophageal but there is no blood in either of the apparent dorsal bifurcations of each vessel. A small transversely placed body resting on the dorsal blood vessel but attached to the anterior face of each septum, from 50/51 posteriorly, resembles the "lymph" glands present in similar locations of certain species of the megascolecine genus, *Pheretima* Kinberg 1866.

Metandric. A longitudinal membrane on each side of the body between 10/11 and 11/12 just lateral to the testes and male funnel looks much like the wall of a testis sac but a roof was not found (testicular coagulum extending well upwards). Seminal vesicles, one pair, in xii, large, lobed. Prostates *ca.* 20 mm long, would reach into xliv at least if straight. A duct is not clearly marked off but may be about 3 mm long. The male deferent duct comes into contact with lateral face of the prostatic duct in xvii but is continued on slightly, somewhat thickened, before turning mesially to pass into the parietes just behind the prostatic duct.

Spermathecae, without diverticula or seminal chambers, *ca.* 6 mm long, flattened against the parietes back to 9/10 and with a slightly wider portion vertically flattened against anterior face of 9/10 to which the spermatheca is bound by connective tissue. Duct and ampulla are not distinctly demarcated ex-

ternally. If an ectal portion with thick wall and very small lumen is to be regarded as the duct, it then is much shorter than the ampulla. A terminal ental portion of the spermatheca is distended by a white coagulum.

Remarks. A tail portion had been recently broken off, presumably during collection. The hind end that was in the same tube may well be of the same worm though the jagged edges of the breaks do not exactly fit together. The clitellum is cracked in several places as often happens when worms are preserved with that organ in maximal tumescence. Except for local macerations of intestinal wall the specimen otherwise is in good condition.

A supra-intestinal gland of any kind has been unknown hitherto in any ocnerodrilid. Its anatomy in *N. magna* needs characterization from microtome rather than freehand sections but now appears to be similar to that of the "grid" at end of the typhlosole in the octochaetine *Barogaster* Gates 1939. Supra-intestinal glands have not as yet been looked for in many earthworm genera. Hitherto the glands usually have been associated with the posterior end of a median typhlosole. In *Nematogenia,* however, the glands are present only when there is no typhlosole.

N. magna is distinguishable from all ocnerodrilids, except two species of *Kerriona* Michaelsen 1924 and one of *Paulistus* Michaelsen 1925, by its size as well as segment number, and from the species of *Kerriona* and *Paulistus* by the presence of two gizzards (instead of none). A size of 260 x 8 mm, in a family where all species hitherto known, except those just mentioned, are 15-60 x 1-3 mm certainly is significant. Recognition of additional differences from other species of *Nematogenia* awaits more adequate characterization of those previously erected.

A species, when understood to be an interbreeding population of organisms with more or less individual if not also geographic variation, obviously cannot be defined from a single individual. Nevertheless, some sort of a concise characterization is needed. In such a precis it is also convenient to list characters, presumably of taxonomic importance, about which information is desired.

Precis. Spermathecal pores minute, superficial, slightly median to *B*, at 8/9. Female pores at sites of missing *a* setae. Male pores at or just lateral to *B* and shortly behind prostatic pores, both pores of a side in an area of special tumescence within a median field reaching laterally into *BC*. Clitellum, annular, on xiv-xxviii. Setae, not closely paired. (Nephropores? No dorsal pores.) Prostomium prolobous. (Pigmentation?) Segments, *ca.* 529. Size, 260 x 8 mm.

Intestinal origin in xii. (No typhlosole.) Supra-intestinal gland in region around 155th segment. Lymph glands present posteriorly. Metandric. Spermathecal duct shorter than ampulla.

Nematogenia dominicana sp. nov.

San Cristobal, Santo Domingo. From earth of damp forested hillside, July 19, 1930, 1-0-0. Damp soil in hills to west, July 20, 1930, 0-1-0. R. Bond per Dr. G. E. Pickford.

External characteristics. Length, *ca.* 195 mm. Diameter, 5+ mm. Segments, *ca.* 675 (No. 2). Pigmentation lacking ("grayish pink or pink, paler posteriorly," collector's note). Prostomium, broadly prolobous (No. 1) or indenting i (No. 2) and then slightly proepilobous. Secondary furrows; one deep and postsetal on each of vii-xiii, one deep and presetal on each of viii-xiii, less obvious pre- and postsetal secondary furrows recognizable back to xl. Each pre- and postsetal secondary annulus of ix-xi has a well marked tertiary furrow. Nephropores unrecognizable. Dorsal pores lacking.

Setae first certainly recognizable on ii or iii, very closely paired, *AB* ca.=*CD*, *BC* much<*AA*, *DD*>½C, in xxv, *BC*: *AA*::5:7 gradually changing to 1:2 posteriorly, and thence on constant.

Spermathecal pores, one pair, at *B*, on 8/9. Female pores unrecognizable but possibly equatorial and in *AB* (*a* present) on xiv. Male and prostatic pores discrete, the former minute, circular, the others transversely slit-like and anterior, all about at *B* on xvii. Porophores transversely elliptical, flat but markedly protuberant, with center about at *B*, reaching into *AA* and to 17/18 but not to 16/17. A distinctly demarcated, smooth, small,

circular portion bearing the prostatic pore appears to be slightly retractile and the immediate margin of the pore is raised in a teat-like protuberance. The male pore is near the posterior margin of the porophore.

No other genital markings.

Internal anatomy. Septum 5/6 membranous, 6/7 slightly muscular, 7/8-11/12 thickly muscular and funnel-shaped.

Gizzards well developed, in vi-vii. Calciferous glands one pair, in ix, of solid type (no lumen), rather heart-shaped, with slight ventral indentation (not disc-shaped). Intestinal origin in xiv (2). Typhlosole lacking and no slightest rudiment recognizable from xiv-xl but from xli to lxvi there is a low, band-like area the wrinkled surface of which contrasts strikingly with the smoothness of other portions of the gut wall. The band gradually disappears but at mD a fine ridging still is recognizable and gradually passes into the supra-intestinal gland, a wide thickening of gut roof also ridged on ventral side. The gland extends from 180/181 to 194/195 (No. 1, *ca.* 365 segments) or from 187/188 to 208/209 (No. 2). The gland is slightly constricted at septal insertions (the juvenile) and has an appearance of being marked off into segmental glands.

Dorsal blood vessel single, disappearing from view in tissue masses of the pharyngeal bulb that reach to 5/6, in intestinal region receiving in each segment two pairs of large vessels from the gut, one pair near each septum. Supra-oesophageal trunk recognizable only in ix-xi, apparently ending with hearts of xi. Extra-oesophageals filled with blood and recognizable only in viii-ix where they are median to the hearts and free from the gut. A large vessel passes out from the supra-oesophageal in ix, on each side, and shortly bifurcates, one branch passing along calciferous duct to and into the gland, the other branch passing down to join the extra-oesophageal. Subneural quite unrecognizable (probably lacking?). Segmental commissures connecting dorsal and ventral trunks quite slender in v-vii, somewhat larger in viii-ix (lateral hearts?). Hearts of x-xi apparently latero-oesophageal but blood present only in the bifurcations that pass to the supra-oesophageal. Lymph glands present and apparently as in *magna*.

Metandric. Seminal vesicles, one pair, in xii. Prostates 18-20 mm long, would reach at least into xliv if straight, pink (formalin developed artefact?). An ectal white portion, slightly slenderer, 1-2 mm long, with marked muscular sheen constitutes the duct. The male deferent duct is thicker behind 16/17, in contact with lateral face of prostatic duct but continued on as in other species and is narrowed again within the parietes.

Spermathecae, 4+ mm long, without diverticula or seminal chambers, but with distinctly demarcated duct and ampulla. The latter, *ca.* 1 mm long, elliptical in cross section, *ca.* twice as thick as ental portion of duct, filled with a white coagulum. Duct, circular in cross section, very shortly and closely looped ectally.

Reproduction. Brilliant irideseence on male funnels and in spermathecal ducts ectally (but not in coagulum of spermathecal ampullae) shows that sperm had been matured and that copulation had been completed, in the larger specimen. Reproduction presumably is sexual and biparental.

Regeneration. Segment length, at 395/396, abruptly becomes very much shorter and so continues posteriorly, as in a tail regenerate.

Remarks. The aclitellate worm had been ruptured in the intestinal region. No signs of postsexual regression were recognized in that worm which may have been preserved prior to development of the clitellum. In that case copulation takes place, as has been suggested for other species, before the clitellum develops.

Absence of a typhlosole and presence of a supra-intestinal gland indicate relationship to *magna* from which *dominicana* is distinguished as follows: By constant close pairing of setae throughout the body as well as other setal characters. Presence of paired male porophores. Intestinal origin in xiv (rather than xii), an important distinction in a family where the origin so very frequently is in xii. Greater length of spermathecal duct relative to that of the ampulla. Further differences may be recognizable when clitellate specimens become available.

Precis. Spermathecal pores minute, superficial, at *B*, on 8/9. Female pores in *AB*? Male pores about at *B*, shortly behind prostatic pores, in paired, transversely elliptical porophores.

(Clitellum?) Setae very closely paired, $BC<AA$, $DD>\frac{1}{2}$C. (Nephropores? No dorsal pores.) Prostomium prolobous. Unpigmented (?). Segments, 675. Size, 195 x 5 mm.

Intestinal origin in xiv. (No typhlosole.) Supra-intestinal gland in ten or more segments behind 180/181. Lymph glands present posteriorly. Metandric. Spermathecal duct longer than ampulla, ectally with short loops.

Nematogenia montana sp. nov.

Loma Rucilla, Cordillera Central, Dominican Republic, under grass in open pine woods at 8-10,000 feet, June 1938, 0-0-2. Dr. P. J. Darlington Jr.

External characteristics. Length, 85 and 108 mm. Diameter, 4 mm (clitellum). Segments, 178 and 144 ($\pm$1, a metamerie anomaly). Pigmentation, unrecognizable (alcoholic preservation). Prostomium, prolobous (2 specimens). Secondary furrows, one presetal and one postsetal each on vii-ix. Nephropores and dorsal pores unrecognizable, the latter probably lacking.

Setae closely paired anterior to clitellum, more widely paired behind clitellum, farther posteriorly AB ca.=or$<CD<BC<AA$, DD=or slightly$<\frac{1}{2}$C.

Clitellum white, annular, from 13/14 onto anterior portion of xxi (No. 1) or to 21/22 (No. 2), intersegmental furrows present (No. 1) or lacking (No. 2), setae probably present.

Spermathecal pores, one pair, about at B, on anterior margin of ix. Female pores, probably slightly anteromedian to a setae, on xiv. Male and prostatic pores unrecognizable but presumably in or near a small indistinctly demarcated white area in AB, on xvii.

No other genital markings.

Internal anatomy. Septa 5/6-11/12 muscular to thickly muscular.

Gizzards well developed, in vi and vii. Calciferous glands, one pair, in ix, of solid type (no lumen), sausage-shaped, opening through a short stalk from dorsal end into oesophagus anterior to 9/10. Intestinal origin in xiii (2). Typhlosole begins rather gradually in region of xvii-xxii, reaching maximum height (0.75 mm) in xxv-xxvi, lamelliform, apparently ending abruptly in lxxxvii (No. 1) or ciii (No. 2) though more careful examination

reveals a rudimentary continuation that gradually diminishes and is unrecognizable behind xcv (No. 1) or cxv (No. 2). Supra-intestinal gland lacking.

Vascular system, with latero-oesophageal hearts in x-xi, no subneural, but with "lymph" glands, and, so far as can be determined, as in *magna*.

Metandric. Seminal vesicles, one pair, lobed, in xii. Prostates *ca.* 14 mm long, would reach at least into region of xxxviii-xl if straight (duct indistinguishable externally), passing into parietes at *B*. Male deferent duct just lateral to prostate in xvii, and only well behind ectal portion of that gland turning mesially to pass, slightly widened, into parietes about at *A* and just in front of level of 17/18.

Spermathecae, without diverticula or seminal chambers. Ampullae, on anterior face of 9/10, clearly demarcated from a slender duct that may be nearly as long as the ampulla or somewhat shorter.

Reproduction. Iridescence on male funnels, in spermathecal ducts and in coagulum of each spermathecal ampulla is brilliant and demonstrates maturation of sperm as well as completion of copulation. Reproduction presumably is sexual and biparental.

Regeneration. The penultimate segment of each worm is large and setigerous. The anal "segment" is unusually small, scarcely more than a narrow band around a vertically slit-like anal aperture. Such an anal band, without pigment, develops in pigmented species shortly after posterior amputation and is quite different at that stage from the normal anal region.

Segment cii of No. 1 is only about half as long as ci and succeeding segments for some distance are of the same length. The region behind 101/102 would have been suspected of being a regenerate except for the increase in length of the last few segments.

Parasites. Cysts are scattered through the coelomic cavities of a posterior portion of the body in one worm.

Remarks. N. montana is clearly distinguished from *magna* by the much smaller size, shorter clitellum, presence of a typhlosole, and absence of a supra-intestinal gland. Distinctions from *dominicana* are: much smaller number of segments, wider pairing of setae behind the clitellum, shorter and unlooped spermathecal

duct, intestinal origin in xiii instead of xiv, presence of a typhlosole, and absence of a supra-intestinal gland. The only differences from the inadequately characterized *panamaensis* that can be cited at present are: greater size (rather than 35-75 x 1-2 mm), larger number of segments (rather than 110-120), absence of dorsal pores, wider pairing of setae behind the clitellum. Presumably closest relationships are with *panamaensis*.

Absence of male funnels, or any rudiments thereof, in segment x of this and the two preceding species appears to be indicative of long establishment of the metandry.

Precis. Spermathecal pores minute, superficial, about at *B*, on anterior margin of ix. Female pores anteromedian to *a* (?). Male pores behind prostatic pores which are also in *AB* (no porophores or male field?). Clitellum, annular, on xiv-xxii. Setae more widely paired behind clitellum, AB=or$<CD<BC<AA$, DD=or$<\frac{1}{2}$C. (Nephropores? No dorsal pores.) Prostomium prolobous. (Pigmentation?) Segments, 144-178. Size, 85-105 x 4 mm.

Intestinal origin in xiii. Typhlosole simply lamelliform. (No supra-intestinal gland.) Lymph glands present posteriorly. Metandric. Spermathecal duct, about as long as ampulla, slender.

Nematogenia alba sp. nov.

Loma Rucilla, Cordillera Central, Dominican Republic, under grass in open pine woods at 8-10,000 feet, June 1938, 1-3-2. Dr. P. J. Darlington Jr.

External characteristics. Length, 95-115 mm. Diameter, 4-4+ mm. Segments, 211, 213, 230. Pigmentation, unrecognizable (alcoholic preservation). Prostomium, tanylobous, a definite transverse furrow across the tongue shortly behind anterior margin of i (2 specimens) produces a condition that can be designated as combined tany- and epiloby. Secondary furrows, one presetal and one postsetal on some or all of viii-xi. Nephropores and dorsal pores unrecognizable, the latter probably lacking.

Setae begin on ii and are closely paired, on xx AB ca.=$CD<BC$ much$<$or=AA, DD ca.=or slightly$<\frac{1}{2}$C.

Clitellum red, annular, on xiii-xx (1), setae present, intersegmental furrows obliterated except that a slight trace of 13/14 is still recognizable in ventrum.

Spermathecal pores, one pair, very small, transverse slits, on or just lateral to *B*, definitely though only slightly behind 8/9. Female pores, minute, diagonal slits, in front of *a* setae. Male and prostatic pores discrete, in seminal furrows. One limb of each furrow is about on *A* between level of 17/18 (unrecognizable in ventrum) and eq/xvii, the other limb passing almost at a right angle laterally along eq/xvii to *B*. The male pore is at the posterior end of the groove. The prostatic pore has not been seen but the prostatic duct has been traced through the body wall to anterior end of the groove. Each seminal furrow is in a small region of special tumescence reaching from about *mBC* median to *A*, to eq/xviii but not to level of 16/17. Both tumescences, on the clitellate worm, are within a single transverse field.

No other genital markings.

Internal anatomy. Septum 6/7 membranous or only very slightly strengthened, (5/6?), 7/8-11/12 slightly muscular and translucent.

Gizzards well developed, apparently in vi-vii. Calciferous glands, one pair, in ix, of solid type (no lumen), ovoidal, with rather short but thick stalk from dorsal apex passing to lateral face of oesophagus anterior to 9/10. Oesophagus valvular through xiii (3). Intestinal origin in xiv (3), the real origin concealed by symmetrical or asymmetrical herniation of intestine through 13/14 well into xiii. Typhlosole rudimentary in xv-xix, gradually becoming lamelliform and attaining maximum height (1 + mm) in xix-xx, gradually losing height posteriorly and unrecognizable behind 158/159 (juvenile with 230 segments), 140/141 (211 segments, posterior amputee?), or 143/144 (213 segments, apparently with a very small anal-segment regenerate) and in this worm ending abruptly rather than gradually and indefinitely. Supra-intestinal gland lacking.

Vascular system with latero-oesophageal hearts in x-xi, no subneural (lymph glands?); otherwise, so far as can be determined, as in *magna*. Nephridia present from ii, ducts (behind the clitellum) pass into parietes in *AB*.

Holandric. Seminal vesicles in ix and xii. Those of ix may be much larger, extending anteriorly into vii but in a worm with right posterior vesicle continued into xv, the left anterior

vesicle is confined to ix. Prostates, 17+ mm long, would reach into lx if straight, elliptical in cross section and with slit-shaped lumen. An ectal portion *ca.* two mm long, with muscular sheen, circular in cross section, with narrower lumen, is the duct. Male deferent duct lateral to the prostate in xvii, posteriorly turning mesially to pass into parietes at level of 17/18 about at *A.* slightly thickened just prior to entrance into parietes.

Spermathecal duct about as long as ampulla from which it is clearly demarcated by a definite constriction, thicker entally and there elliptical in cross section, with a slit-shaped lumen, ectal portion circular in cross section and with much smaller lumen. Coagulum that fills the ampulla is without iridescence. The iridescence that characterizes the ental portion of the duct is recognizable in transverse sections only in a jagged circle apparently at the middle of the wall.

Reproduction. Brilliant iridescence on male funnels and in ental portions of spermathecal ducts (aclitellate and clitellate worms) shows that sperm had been matured and that copulation had taken place. Reproduction presumably is sexual and biparental.

Remarks. The clitellum of one worm listed as clitellate actually is only slightly developed.

Prostates of one worm pass straight forward into viii instead of posteriorly as usual.

The cuticle was found, several years after the Hispaniolan worms were dissected, to be loosened from the epidermis in various small portions of the body. Removal of loosened patches permitted, in better conditions, another search for nephropores. None was found in three species. Possible sites in *N. alba* may be as follows: At or slightly above *D* and near anterior segmental margins, on iii-ix or x. Posteriorly, on segmental equators (but with some irregularity?) and just median to *D.*

Male maturity, here as in *dominicana,* apparently may be reached and copulation completed before appearance of the clitellum. The latter organ, at full development, is indicative primarily of female maturity. Copulation may even be a prerequisite for clitellar development.

N. alba is distinguished from all species hitherto referred to the genus by its holandry, from all American species by the

presence of seminal grooves, and, with exception of *montana*, by the presence of a typhlosole. Further distinctions from *montana* are provided by the intestinal origin in xiv, and the prostomium.

Precis. Spermathecal pores small transverse slits, at or just lateral to *B*, slightly behind 8/9. Female pores in front of *a*. Male pores in posterior ends of seminal grooves, about at *A* and 17/18. Male field transverse, seminal grooves along *A* from 17/18 to eq/xvii and thence to *B*. Clitellum, annular, on xiii-xx. Setae, closely paired, *AB*=*CD*, *BC*<or=*AA*, *DD* ca=½C. (Nephropores? No dorsal pores.) Prostomium tanylobous but with tongue crossed by a transverse furrow. (Pigmentation?) Segments, 211-230. Size, 95-115 x 4 mm.

Intestinal origin in xiv. Typhlosole vertically lamelliform. (No supra-intestinal gland. Lymph glands?) Holandric. Seminal vesicles in ix and xii. Spermathecal duct about as long as ampulla, thicker entally.

Nematogenia lacuum Beddard, 1893

Pygmaeodrilus lacuum Beddard 1893, Quart. J. Micr. Sci., 34, p. 259, figs. 13-16 (pl. 26). (Type locality, supposedly Lagos in West Africa. Types, if extant, in the British Mus.)

Oenerodrilus lacuum, Beddard, 1895, Monog. Oligochaeta, p. 515.

Nematogenia lacuum, Michaelsen, 1900, Das Tierreich, 10, p. 376.

This taxon, unfortunately, was made the type species. It is known only from the original description of "five or six" specimens supposedly from Lagos (West Africa) but collected alive at Kew in England. The anatomy was determined from sections partly ruined by sand which presumably had not been cleared out from the gut. No information is available as to nephropores, female pores, male field, typhlosole, supra-intestinal glands, major blood vessels, hearts.

The species always has been assumed to be endemic in Africa.

Precis. Spermathecal pores in *AB*, at 8/9. (Female pores?) Male pores, apertures of united male deferent and prostatic ducts, in *AB*, in oval elevations in xvii. Clitellum, saddle-shaped, on xiii/2-xxvi/2. Setae closely paired, *ab*/xvii-xviii lacking. (Nephropores?) Dorsal pores present, beginning at 6/7 or even anteriorly. Prostomium prolobous(?). (Pigmentation?) Segments, *ca.* 120. Size, 25 (x 1+?) mm.

Intestinal origin in xii. (Typhlosole? Supra-intestinal gland? Lymph glands? Hearts?) Metandric. Seminal vesicles in xii. Small bulbus ejaculatorius present.

Spermathecal duct slender, longer than the ampulla.

Distribution. Unknown. (See above.)

Nematogenia panamaensis Eisen, 1900

Oenerodrilus (*Nematogenia*) *lacuum* var. *panamaensis*, Eisen 1900, Proc. California Ac. Sci., (3) 2, p. 127, figs. 55-65 (pl. 9), 114-116 (pl. 11). (Type locality, Panama. Types, if extant, probably in U. S. Nat. Mus.)

Nematogenia panamaensis, Michaelsen, 1900, Das Tierreich, 10, p. 376.

Nematogenia panamaensis, Michaelsen, 1903, Ark. Zool. 1, p. 163. (Cameroons)

Nematogenia panamaensis, Michaelsen, 1904, Sitzber. Böhm. Ges. Prag, 1903, (40), p. 16. (Ceylon)

Nematogenia josephina Cognetti, 1904, Boll. Mus. Torino, 19, (478), p. 3. (Type locality, San Jose, Costa Rica. Types in Torino Mus.?)

Nematogenia josephina, Cognetti, 1906, Mem. Ac. Sci. Torino, 56, p. 55.

Nematogonia (*sic*) *panamaensis*, Cognetti, 1908, Ann. Mus. Genova, (3), 4, p. 33. (Fernando Po)

Nematogenia panamaensis, Michaelsen, 1915, Ergeb. 2 Deutschen Zentral-Afrika-Exp. 1910-11, 1, (Zool. 1), p. 222. (Belgian Congo)

Nematogenia panamaensis, Stephenson, 1923, Oligochaeta, in Fauna British India, p. 483.

Prostomium, female pores, typhlosole, lymph and supra-intestinal glands, hearts and other portions of the vascular system, in the original description, were not mentioned. Nor have most of those deficiencies as yet been rectified. A blood vessel in segment xii is indeed labelled heart (Eisen, 1900, fig. 56h, pl. 9) but none was shown in xi where a pair certainly is present. Hearts in xii, in the Ocnerodrilidae, would be so unusual that abnormality or a mistake in drawing must, in absence of subsequent confirmation, be assumed.

Male pores are discrete. Hence, a statement to the contrary (and applicable only to *lacuum*) in the generic definition always has been unwarranted.

Sperm were seen by Eisen in the spermathecal ampulla. Reproduction, since sperm are matured and exchanged in copulation, can be assumed to be sexual and biparental.

N. josephina is distinguished from *panamaensis*, according to its author (Cognetti, 1906, p. 57) by location of the first dorsal

pore (at 8/9 instead of 10/11), length of prostates, and absence of hearts in xii. The first two characters, in better known species, are subject to considerable individual variation and the third difference probably is not real. If spermathecal pores were correctly located by Cognetti, at 8/9, there would be reason for believing some distinct status eventually might be justified.

N. panamaensis is peregrine, in the sense usually intended by that word in oligochaetological literature, the overseas discontinuities in its distribution due to transportation, presumably by man and since the days of Henry the Navigator. The discrete male pores (if valid evidence of relationship) then require, instead of an African origin as previously maintained, one in America.

Precis. Spermathecal pores in *AB*, midway between 8/9 and eq/ix. (Female pores anterior to *a*?) Male pores behind prostatic pores, in a single pair of porophores. Clitellum (shape?), in xiii, xiii/n, xiv-xxi, xxii/n. Setae, closely paired, *a,b*/xvii lacking. Nephropores at *D*. Dorsal pores beginning at or behind 8/9. (Prostomium? Pigmentation?) Segments 110-120. Size, 37-55 x 1-2 mm.

Intestinal origin in xiii. (Typhlosole? Supra-intestinal and lymph glands?) Metandric. Spermathecal duct slender, shorter than ampulla.

Distribution. Panama, Costa Rica (San Jose), Cameroons (Bange, Bibundi, Buea, Victoria, Musake), Fernando Po, Belgian Congo (Kongo da Lemba and St. Joseph on the Luala River), Ceylon (Peradeniya).

*Key to genera of the Ocnerodrilidae**

1. *a.* Extramural calciferous glands lacking ...2
   b. Extramural calciferous glands present 3
2. *a.* One gizzard, in vii ..... *Malabaria, Thatonia.*
   b. Two gizzards, in vi-vii ..... *Deccania.*
3. *a.* Calciferous sacs paired, lateral 4
   b. Califerous sacs unpaired, median and ventral 8

* *Malabaria, Thatonia, Deccania* are known only from India and Burma *Mahcina* only from the Seychelles (to which it may have been transported recently), *Curgiona* only from India (to which it may have been introduced recently), *Gordiodrilus* (as of Michaelsen & Stephenson) is African. Other genera are American or American and African.

4. *a.* Calciferous sacs in ix and x 5
   b. Calciferous sacs in ix only 6
5. *a.* One gizzard, in vi ..... *Maheina.*
   b. No gizzard ..... *Paulistus, Quechuona.*
6. *a.* One or more gizzards 7
   b. No gizzards ..... *Octocrodrilus,* including *Liodrilus, Haplodrilus, Ilyogenia,* as well as *Pygmaeodrilus, Eukerria* (part), *Diaphorodrilus, Kerriona.*
7. *a.* One gizzard, in vii ..... *Eukerria* (as it must be restricted).
   b. Two gizzards, in vi-vii ..... *Nematogenia.*
8. *a.* Calciferous sacs in ix-x, (gizzard in vii) ... *Curgiona.*
   b. Calciferous sacs in ix 9
9. *a.* One or more gizzards 10
   b. No gizzard ..... *Gordiodrilus* (part), as it must be restricted.
10. *a.* One gizzard, in viii ..... *Gordiodrilus,* a "*robustus*" group of species.
    b. Two gizzards, in vii-viii ..... *Gordiodrilus,* a "*nannodrilus*" group of species.

DISCUSSION

A taxonomy based primarily on genital structure culminated, in the Ocnerodrilidae, in the congeries known as *Gordiodrilus* (cf. Gates, 1942b, pp. 75-85). That taxonomic waste-basket which defeated Stephenson, "I can do nothing with this heterogeneous group" (1930, p. 863), probably could have been avoided (Gates, 1942b, p. 76) if somatic structure had been taken into consideration, even as little as previously. Collections that would justify a real attempt at revision of *Gordiodrilus*, unfortunately, are no more available now than in 1942.

Errors of typography, observation and interpretation, so frequent in the literature on *Gordiodrilus*, may well be much less common in the literature on other ocnerodrilid genera. Nevertheless, more adequate characterization of somatic systems still is

prerequisite to a revision of any portion of the family. Also needed is information as to individual and geographical variation about which next to nothing is now known.

Some of the taxonomic changes that will be made in the future can be deduced from a key constructed entirely on characters supplied by just one somatic system. That is the digestive system. The organs involved are gizzards and calciferous glands, with the glands having the greater importance.

Genera that key out together are presently distinguishable from each other only by means of characters furnished by the system usually most liable to rapid evolutionary change. The genital characters by which those genera are defined and distinguished, elsewhere in the family and/or in other families, do not, and sometimes cannot, have that taxonomic value.

Relationships suggested by somatic systems are of course often different from those that were deduced in the past from reproductive structure. Thus *Diaphorodrilus* now seems to be closer to *Ocnerodrilus* than to *Gordiodrilus* with which it was mistakenly united. *Kerriona* may be closer to *Ocnerodrilus* than to its supposed ancestor *Kerria*.

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TRIASSIC REPTILE FOOTPRINT FAUNULES FROM MILFORD, NEW JERSEY

By Donald Baird

With Four Plates

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

November, 1957

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No. 5 — *Triassic Reptile Footprint Faunules from Milford, New Jersey*

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FOREWORD

In a recent paper Wilhelm Bock (1952) has described a number of important faunules of fossil footprints from various horizons and localities in the Upper Triassic (Middle Keuper) of the Newark Basin. One of these faunules, found in a gray sandstone layer of the upper Brunswick formation near Milford, New Jersey, had been discussed in the literature as early as 1886; but until 1952 only its dominant species, *Chirotherium parvum*, had been adequately described. In the same paper

Bock described a new species of pseudosuchian footprints, *Chirotherium lulli,* found in a reddish-brown siltstone bed at the same locality. More recently a slab bearing the counterpart trackway of *C. lulli* and two forms of dinosaur tracks has come to light and, with Bock's generous permission, has been described (Baird, 1954).

Most of the Milford footprints discussed by Bock had been collected by John Eyerman in 1885 and deposited in the geological museum of Lafayette College at Easton, Pennsylvania (hereafter abbreviated LC). One slab, privately owned, had been acquired by Bock for the Academy of Natural Sciences of Philadelphia (ANS). While Bock's paper was in press, Eyerman's second and much larger collection from the same quarries came to light in the Museum of Comparative Zoology (MCZ), and received independent preliminary study. This material, though described in part by Eyerman in 1889, had been overlooked by subsequent authors. A search of the American Museum of Natural History collections (AMNH) has produced eight additional footprint-bearing slabs collected at Milford by Eyerman in 1886.

Besides increasing the *Chirotherium parvum* faunule by several species and permitting morphological re-interpretation of those already described, the additional material includes a new species of dinosaur footprint which represents a third Milford faunal horizon. As this material also explains certain 19th-century misidentifications which have distorted the faunal picture, and the geological correlations which have been based on it, I have undertaken a comprehensive re-examination of the Milford reptile footprints and their zoological and stratigraphic significance.

I am particularly indebted to Wilhelm Bock for photographs and for permission to mold the type of *Chirotherium copei,* to J. L. Dyson for the loan of the Lafayette College types, and to E. H. Colbert for the loan of American Museum specimens and for generously making available his unpublished data on *Coelophysis.* Special thanks for the privilege of studying the collections under their care are due to G. W. Bain, A. E. Wood, and R. E. Schortmann at Amherst, R. G. Chaffee at Dartmouth, E. H. Colbert and Mrs. R. H. Nichols at the American Museum, D. H. Dunkle at the U. S. National Museum, J. T. Gregory at Yale, J. L. Kay at the Carnegie Museum, and C. W. Waldron,

Jr. at the Museum of Science, Boston. For their helpful and stimulating suggestions I am pleasantly indebted to C. L. Camp, E. H. Colbert, the late R. S. Lull, the late J. H. McGregor, F. E. Peabody, and D. M. S. Watson. The continued support and encouragement of Dr. Alfred S. Romer, as well as his critical reading of the manuscript, are most gratefully acknowledged.

GEOLOGICAL OCCURRENCE

Two distinct footprint horizons bearing mutually exclusive faunules occur in the gray sandstones of the Milford quarries. Eyerman nowhere indicates the relative stratigraphic positions of these horizons, but they are probably not very widely separated: both are referred to the upper Brunswick formation, about 5,100 meters above the Triassic base. For clarity they are here arbitrarily designated Levels A and B. Although this cannot be stated as certain, Eyerman's discussion of the MCZ material (1889, p. 32) implies that the Smith Clark quarry was the source of the Level B or *Chirotherium parvum* faunule, while another quarry about one-half mile to the east furnished all the material from Level A.

At Level A, the footprints were impressed in gray shale and are preserved as natural casts on the under surface of a gray sandstone 4 to 6 cm. thick. The upper surface of this sandstone is irregularly excavated into shallow pockets in which adhere pieces of the overlying gray shale. All the footprints are referred to a single species, *Grallator sulcatus*. Most are deeply impressed, between 1 and 2 cm. below surface level at their deepest points; many are obscured by slippage, overlapping, or slumping of the extruded clay. None shows impressions of the plantar scales and very few show fringe-scale striations. Among the tracks on MCZ 216 is a striated drag-mark 25 mm. wide by 2 mm. deep, flanked on either side by intermittent shallow scratches. This might be interpreted as a tail-trace but is more probably the drag-mark of a Triassic conifer or horsetail rush. Very similar marks in the *Chirotherium* sandstone of Thüringen have been described as drag-marks of *Equisetites* by Rühle von Lilienstern (1939, p. 370, pl. 12). Narrow shrinkage cracks, rarely more than 5 mm. wide, characterize Level A.

Level B, which carries the larger faunule, somewhat resembles A in lithology. The sandstone overlying the recording surface, however, quarries out in layered flagstones 1.5 to 3.5 cm. thick; the flat upper surfaces typically bear shallow ripples and run-off marks. Shrinkage cracks of variable width are common. Raindrops have pitted both ground surface and footprints, obscuring the plantar surfaces; but the sides of several deeper tracks show striated claw-marks and fringe-scale furrows. Certain parallel series of sharp, shallow scratches may be of arthropod origin, but no trackway sequences are preserved. Annelids have perforated the layers after deposition; their sand-filled burrows loop down into the shale or course along the sandstone-shale interface, looking superficially like dasycladacean algae. To the Milford flora recorded by Bock (1952, 1952 A) may be added the genus *Neocalamites* (MCZ 211). Several slabs bear branching or reticular patches, presumably algal.

The third Milford footprint horizon, discussed in my previous paper (1954), lies in a reddish-brown siltstone which crops out in the Smith Clark quarry some 15 meters above Level B. Reptile footprints of pseudosuchian appearance occur at another horizon in that quarry but are unfortunately too vague and fragmentary for adequate characterization (see Bock, 1952, pl 49, fig. 8).

The stratigraphic correlation of these beds with those of southeastern Pennsylvania, the Connecticut Valley, and central Europe will be discussed after an analysis of the fauna.

SYSTEMATIC DESCRIPTIONS

Nineteenth-century publications on the Milford footprints are so vague, confused, and contradictory that little faith can be placed in them. The foundations of Triassic ichnology had been so monumentally laid by Edward Hitchcock that footprints from any part of the Newark series were customarily identified by reference to Hitchcock's figures of species from the Connecticut River Valley. This practice led inevitably to confusion, for the classic Connecticut Valley faunas actually have little in common with those of Pennsylvania and New Jersey. As the nomenclature of Triassic footprints evolved, faunal revisers changed the names of Milford species without checking the determina-

tions. For brevity, the terminologies of earlier authors and of this paper are summarized in Table 1.

Before Bock's restudy, only C. H. Hitchcock (1889) had erected new species for Milford footprints. His descriptions, unaccompanied by figures, are so vague that of the species mentioned only one, *Chirotherium* [*"Otozoum"*] *parvum*, can be identified positively. His new species *"Chimaerichnus ingens,"* characterized only as "two relief tracks of considerable size and representing only one-half of the foot," is a nomen nudum. Any nomenclatural questions arising from C. H. Hitchcock's work have, fortunately, been settled by Bock's designation of types.

Order SAURISCHIA

Suborder THEROPODA

Infraorder COELUROSAURIA

Form-family GRALLATORIDAE Lull, 1904

(=ANCHISAURIPODIDAE Lull, 1904)

Genus GRALLATOR E. Hitchcock, 1858

Type species *G. cursorius* E. Hitchcock (1858, p. 72) designated by Lull (1904, p. 494).

GRALLATOR SULCATUS Baird, n. sp.
Figure 1; Plate 1, figure 1.

Type. MCZ 215, a left pes imprint.

Hypodigm. MCZ 215-228 inclusive, slabs bearing 37 pes imprints; AMNH 1982 and 1983, 6 imprints; LC S487, parts of 3 overlapping imprints. All collected by John Eyerman, 1885-1887.

Horizon. Upper Triassic (Middle Keuper), Newark series, upper Brunswick formation. Level A.

Locality (*fide* Eyerman, 1889, p. 32). Quarry of the Messrs. Clark about one-half mile east of the Smith Clark quarry, near Milford, Hunterdon County, New Jersey.

TABLE 1: ATTEMPTED SYNONYMY OF MILFORD FOOTPRINTS

Dashes indicate derivation from a previous author.

EYERMAN, 1886	C. H. HITCHCOCK, 1889	EYERMAN, 1889
LEVEL A:		
aff. Anomoepus major		Brontozoum isodactylum
		Grallator cuneatus
	[?] Grallator parallelus — — — — — — — — — — — — — — — —	
	[?] Grallator cuneatus — — — — — — — — — — — — — — — —	
LEVEL B:		
	[?] Grallator cuneatus	
	[?] Grallator gracilis — — — — — — — — — — — — — — — —	
		[?] Grallator tenuis
aff. Anomoepus major	Otozoum parvum, n. sp.	
		Anomoepus minor — —
	[?] Chimaerichnus ingens, n. sp. — — — — — — — — — — — —	
	[?] Polemarchus gigas — — — — — — — — — — — — — — — —	
	Argozoum dispari-digitatum — — — — — — — — — — — — — —	

Diagnosis. A moderately large *Grallator,* differing from other species in the anterior position and relative shortness of digit III and in having the bases of II and III closely united, while IV is separated from III by a pronounced sulcus which extends back to the metatarso-phalangeal pad of III. Ovoid metatarso-phalangeal pads of II and IV regularly and equally impressing, that of II more anterior. Second phalangeal pad of II opposite first pad of III. Trackway characters unknown.

Measurements. Defects of impression and preservation make impossible a valid and consistent suite of measurements. Dimensions of the best-preserved specimens, however, suffice for descriptive if not for statistical treatment. Measurements of the type, adjusted for slippage and a transverse crack-filling, are as follows:

LULL, 1915	BOCK, 1952	BAIRD, 1957
Anchisauripus parallelus Grallator cuneatus ———	Grallator	Grallator sulcatus, n.sp.
Grallator gracilis ———	Gigandipus ? (Anchisauripus) milfordensis, n.sp. Grallator gracilis	Anchisauripus milfordensis
		Anchisauripus parallelus
		Genus incertum
?Chirotherium parvum	Chirotherium parvum Chirotherium copei, n.sp.	Chirotherium parvum
		Chirotherium eyermani, n.sp.
Sauropus barrattii ——— Sauropus ingens Polemarchus polemarchius	Otozoum (?) lineatus, n.sp. Sauropus barrattii	Apatopus lineatus, n.gen.
Argoides macrodactylus ———————————		(Unidentifiable) Rhynchosauroides hyperbates, n.sp.

Pes, digit no.	II	III	IV
Length, mm.	54	72	59
Length including metatarso-phalangeal pad	78	98	84

Length of pes, 100 mm.; including metatarso-phalangeal pads, 123 mm.; width, 60 mm.

Measurements of digit divarication will vary greatly in a single footprint depending on one's reference points. In the type specimen the angles between axes drawn through the centers of claw base and metatarso-phalangeal pad are: II-7°-III-19°-IV. *Grallator sulcatus* footprints, however, show quite a range of divarication values. In my experience linear and angular measurements such as these have a very limited value for the diagnosis and differentiation of theropod footprints.

Morphology. The abundance of deeply-impressed footprints of this species affords an unusually clear picture of its foot structure, including the relationship of the distal ends of the metatarsals which is rarely recorded in *Grallator* trackways. As in other theropod dinosaurs and in most cursorial birds the

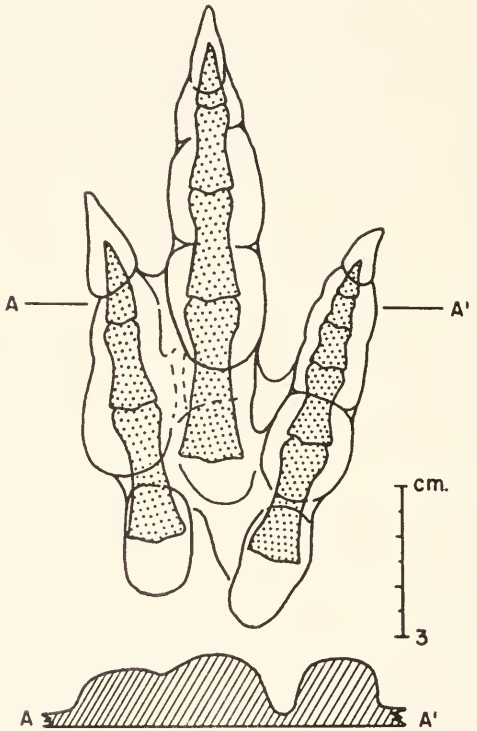


Fig. 1. *Grallator sulcatus* n. sp., x ⅔. Composite outline based on the four best-preserved specimens. Section A-A′ across the inverted natural cast shows the close association of digits II and III and the sulcus separating digit IV. Proximal phalanges of the restored skeleton appear foreshortened.

gait was digitigrade with most of the body weight falling on the joints between the first and second phalanges of digits II, III, and IV. Nevertheless, the pads which underlay the joints between metatarsals and phalanges of digits II and IV impressed

regularly, though less deeply than the digital pads, even in shallow imprints. Apparently this Brunswick species had not achieved the advanced degree of digitigrady shown by later inhabitants of the Connecticut Valley. Unfortunately the lack of trackway measurements precludes any useful comparison between gait patterns of Brunswick and Connecticut Valley Grallatoridae.

The claws of *Grallator sulcatus* are acuminate in some individuals but blunted by wear in others. Regardless of depth of impression the claws were always extended, rather than flexed as in the other Milford theropods; in particularly deep tracks the exaggerated depth of claw-marks is due not to flexure but to pivotal down-turning as the posterior part of the foot was raised.

The slightly domed phalangeal pads coalesce to form a sole callus which appears to have been slightly wider than the toe proper, as in many cursorial birds. The three metatarso-phalangeal pads, though they impressed less deeply, form an integral part of the sole and are separated from the phalangeal pads only by shallow sulci. The close union of digits II and III and the broad separation of IV differentiate *Grallator sulcatus* strikingly from its congeners, in which the digits are either laterally equidistant or III and IV are more closely appressed than II and III.

Variation. Footprints from Level A reveal a sobering degree of variability both in apparent form and in manner of impression. An increased divergence of the lateral toes is less common than an exaggerated out-turning of the claws alone. Whether this out-turning reflects some lateral flexibility at the ungual joint, or merely individual variation in the plane of a horizontally immobile joint, cannot be determined without trackways showing successive imprints of the same foot. Distorted deep impressions reveal that the lateral toes were spread apart as the foot sank into the mud and were contracted again in birdlike fashion as the foot was withdrawn.

Many of the footprints are so deformed by accidents of impression that they give a decidedly erroneous picture of the foot structure. Such anomalies serve to emphasize the dangers involved in any attempt to characterize and interpret footprint species without adequate quantities of well-preserved material.

A footprint is not an organism but the by-product of dynamic contact between an organism and its environment. The all-too-common typological analysis of isolated examples cannot be expected to yield zoologically significant information.

Osteology. Heilmann (1927, p. 179 ff.) and Peabody (1948, p. 399 ff.) have independently concluded that in the Grallatoridae the phalangeal pads must have underlain the joints. This is the situation in many cursorial birds, in which only the ungual joint may coincide with a transverse crease. The osteological restoration of *Grallator sulcatus* in Figure 1 conforms to this principle but differs enough from the examples cited by Heilmann and Peabody to require explanation. In my opinion the pes of *Procompsognathus* which Heilmann (1927, fig. 130 K) has superimposed on the footprint of *Grallator tenuis* would fit a great deal better if the foot were advanced until the ungual joints of digits II and III corresponded with the distal pads instead of their creases. All the joints would then line up neatly opposite pads, with both ends of the fourth phalanx of digit IV included in the distal pad. Except for the over-long claws of *Procompsognathus,* foot and footprint correspond well in structural pattern.

The otherwise convincing skeletal restoration of *Grallator cursorius* in Peabody's figure 37 B shows a crease coinciding with the joint between phalanges 3 and 4 of digit IV. Here again I would prefer to enclose both ends of phalanx 4 in the distal pad: and this is readily done if we use Hitchcock's original figure of the footprint (1858, pl. 13, fig. 3), in which the distal pad appears longer and more square-shouldered like that of *G. tenuis.* Other Triassic theropod footprints such as *Anchisauripus* and *Eubrontes* definitely have a long distal pad on digit IV, and an occasional median constriction of this pad suggests that two joints are actually represented. When the bones of any of these footprint types are restored on the plan advocated here, the phalangeal pattern is precisely that of Triassic and later theropods: the phalanges of digit IV are short, stout-shafted, and successively decreasing slightly in size.

No trace of a hallux is visible in any *Grallator sulcatus* footprint even where the metatarso-phalangeal pad of digit II is impressed as deeply as 14 mm. Obviously the hallux, while presumably present, was vestigial and completely non-functional.

The lengths of the proximal phalanges, usually indeterminate in more digitigrade coelurosaur footprints, can be estimated with fair accuracy from the positions of the regularly impressed metatarso-phalangeal pads. Pads II and IV are impressed to equal depths, differing only as one side of the footprint is deeper than the other. This situation contrasts sharply with that in other species of *Grallator* and in *Anchisauripus* and some species of *Eubrontes,* where the metatarso-phalangeal pad of digit II impresses less deeply or not at all. From this anomaly we may obtain some clue to the probable structure of the metatarsus.

If a Newarkian coelurosaur such as *Podokesaurus* is restored in a walking pose based on *Grallator* trackways (cf. Von Engeln and Caster, 1952, fig. 277), the metatarsus slants forward and downward at an angle of some 115° to the ground plane as the foot is implanted. As the metatarso-phalangeal pads were evidently developed to cushion the sole against the thrust transmitted down the metatarsus, and as they served this function only during implantation and the beginning of the propulsion phase, it follows that the position of their imprints is (broadly speaking) that of projections of the cross-sectional areas of their respective metatarsals when in the implantation position. If this be the case, as comparison with cursorial birds suggests, then the type of transverse arching of the metatarsal bundle at its distal end determines whether pad II or pad IV, or neither, makes the more posterior impression. Similarly, the relative length of the lateral metatarsals plus the thickness of their underlying pads determines the relative depth of the pad impressions. Of course the relative thickness of the pads is unknowable, but where the imprint of pad II is shallow or absent (as in most Newarkian theropod footprints) metatarsal II was probably shorter than IV. Conversely, the dinosaur represented by *Grallator sulcatus* appears to have had lateral metatarsals of approximately equal length.

Among Upper Triassic coelurosaurs metatarsal II is decidedly shorter than IV in *Procompsognathus,* but the lateral metatarsals are equal or subequal in *Ammosaurus, Halticosaurus* and *Coelophysis.* For comparison with *Grallator sulcatus* let us restore from their pedal skeletons the footprints that would have been made by two of these coelurosaurs.

Halticosaurus liliensterni, a massive species from the Knollenmergel of Thüringen, is described by Huene (1934) as having lengths of 20.5, 22, and 20 cm. for metatarsals II, III, and IV; digit I is unknown. To show the relative positions of the digits in walking pose we must make a three-dimensional reconstruction of the pes; when this is projected onto a horizontal plane

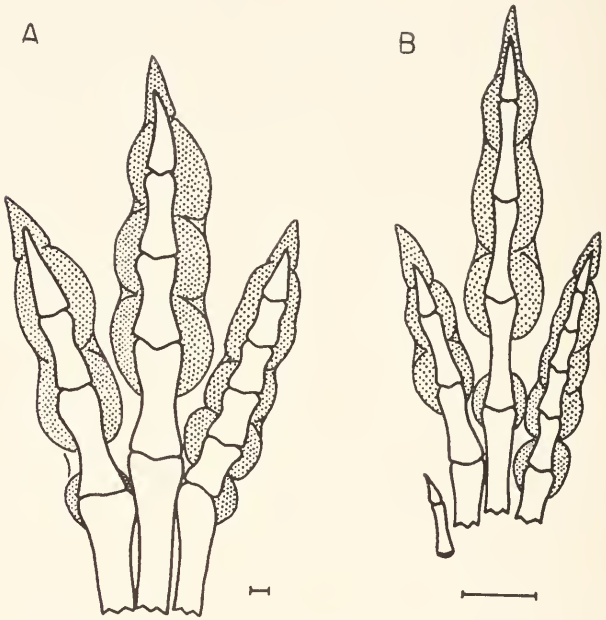


Fig. 2. Reconstructed right pedes of Keuper coelurosaurs, with restored footprints. **A.** *Halticosaurus,* x ¼. **B.** *Procompsognathus,* x 1. Data from Huene.

(analogous to a footprint-recording surface) the metatarsals and proximal phalanges are properly foreshortened (Figure 2 A). Structures in the metatarso-phalangeal region indicate a foot with a moderately compact base and strongly divergent digits; the bulk of the animal and the proportions of the metatarsus suggest that the posterior pads impressed regularly and to nearly equal depths. The positions of the plantar pads are deduced from the skeleton and a plausible reconstruction of their

original form can be derived from Connecticut Valley footprints of equivalent size.

The footprint thus restored is certainly neither a *Grallator* nor a *Gigandipus*, and apparently not an *Anchisauripus* sensu stricto. In *Eubrontes giganteus* and *Anchisauripus minusculus* we find the closest similarities in size, relative lengths of digits and phalanges, and regular and subequal imprints of the metatarso-phalangeal pads. Without venturing any positive correlation we can say that these footprints may well have been made by coelurosaurs of the *Halticosaurus* type.

Procompsognathus triassicus from the Stubensandstein of Württemberg is, in contrast to the hulking *Halticosaurus*, a graceful and diminutive species. When reconstructed (from Huene, 1921) and projected as before (Figure 2 B), its foot appears strikingly slender and laterally compressed. Neither the hallux nor metatarso-phalangeal pad II normally made contact with the ground. The restored footprint is obviously that of a *Grallator* closely comparable to a small *G. cursorius* but having a relatively shorter central digit. If the divarication were larger and the lateral digits somewhat shorter, correlation with a small *G. tenuis* would be indicated.

A comparison of Figures 1 and 2 shows clearly that, even disregarding size, *Grallator sulcatus* has much stronger resemblances to *Procompsognathus* than to *Halticosaurus*. So far as osteology can be inferred from the footprint, only size, minor differences in digital proportion, and the shortness of metatarsal II distinguish *Procompsognathus* from the Milford trackmaker.

Unpublished data on skeletons of *Coelophysis* from the Upper Triassic of New Mexico, made available for this study through the courtesy of E. H. Colbert, show that the foot of that genus is essentially similar to that of *Procompsognathus* except that the lateral metatarsals are equal in length. *Coelophysis* thus closely approximates in structure the reconstructed skeleton of *Grallator sulcatus*. While no positive correlation can be made, the Level A footprints attest the presence of a *Coelophysis*-like coelurosaur in the Newark basin of deposition.

Form-Family GRALLATORIDAE Lull, 1904

Genus ANCHISAURIPUS Lull, 1904

Type species *A. sillimani* (E. Hitchcock), 1843.

ANCHISAURIPUS MILFORDENSIS (Bock)
Figure 3 A

Gigandipus ? (*Anchisauripus*) *milfordensis* Bock, 1952, p. 403; pl. 43, fig. 3 (in legend, for "No. 15210" read S488).

Type. LC S488, a left pes imprint slightly distorted by the paratype pes of *Chirotherium parvum.*

Hypodigm. The type and two other imprints on the same slab; MCZ 135 and 229; AMNH 1981 and 1984. These seven imprints collected by John Eyerman, 1885-1887.

Horizon. Upper Triassic (Middle Keuper), Newark series, upper Brunswick formation about 5100 meters above the Triassic base. Level B.

Locality. Smith Clark quarry near Milford, Hunterdon County, New Jersey, 1.25 km. north of Delaware River bridge.

Tentatively assigned. Certain tracks from the Gettysburg shale (a Brunswick equivalent) near Goldsboro, York County, Pennsylvania (Wanner, 1889, pls. 6, 7, 10). This material was accessioned by the U. S. National Museum in 1888 but is now lost, so that precise comparisons are impossible.

Diagnosis. A small, short-footed, broad-based species. The base of claw II lies opposite the crease between the first and second phalangeal pads of digit III, and the tip of claw IV opposite the distal part of the second pad. Metatarso-phalangeal pads II and IV circular and strongly domed, IV nearly twice the size of II. Claws habitually flexed, hastate in outline with basal recesses.

Morphology. Collation of the new hypodigm permits some amplification and emendation of Bock's description. Removal of some of the obscuring underclay reveals that the structure which Bock interpreted as a semi-rotated hallux is actually a filled shrinkage-crack which runs from the margin of the slab through metatarso-phalangeal pad II of the type, narrows abruptly, and passes under the label and into the manus of *Chirotherium parvum.* Nowhere is there evidence of a hallux imprint, even

in MCZ 135 where the first phalangeal pad of digit II impressed to a depth of 11 mm. This fact and the osteological differences listed in Table 2 preclude assignment of the species to *Gigandipus*.

Individual variation is apparent in even this small sample. MCZ 135 in particular differs from the others in its relatively shorter digit IV, its large size (103 mm. long vs. 93 mm. in

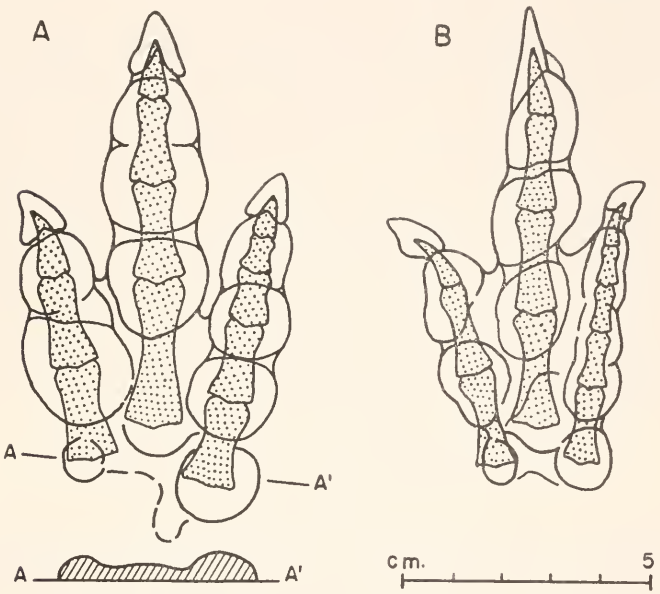


Fig. 3. **A.** *Anchisauripus milfordensis* (Bock), x 3/4. Composite outline based on all seven Milford specimens, drawn the size of S488 or MCZ 229. Section A-A′ shows the domed lateral metatarso-phalangeal pads. **B.** *Anchisauripus parallelus* (Hitchcock), AMNH 1789, x ¾.

the smallest individual, the type), and its angles of digit divarication (II-13°-III-10°-IV vs. II-15°-III-9°-IV in the type).

The outstanding features of the species — the broad-based foot, the broad, rounded phalangeal pads, and the flexed, hastate claws — have been adequately discussed by Bock. Metatarso-phalangeal pad III is ill-defined, but the dome-like lateral pads are impressed to approximately equal depths with reference to

the rest of the foot. The lack of creases between the phalangeal pads suggests the thick, relatively inflexible plantar padding of a foot which is so specialized for cursorial habits that it retains very little power of grasping. Fringe scales on the median side of digit III are represented by parallel striae, somewhat irregularly spaced, which average 10 to the centimeter. They tell little about the squamation but at least prove that the full width of the digit is recorded.

Osteology. A close comparison of Figures 1 and 3 A reveals significant differences in the restored skeletal structure. The individual phalanges of *Anchisauripus milfordensis* are relatively shorter than those of *Grallator sulcatus,* and the unguals may have been, like the claws, shorter and blunter. More important is the difference in the relative positions of the digits. While in *G. sulcatus* the joint of ungual IV lies opposite the joint between phalanges 1 and 2 of diigt III, in *A. milfordensis* it lies opposite the waist of phalanx III-2, and the joint between phalanges 1 and 2 of digit III is aligned with the waist of phalanx IV-3. Clearly the central digit of *A. milfordensis* is less advanced with respect to the lateral digits. Additional osteological criteria for comparing this species to other dinosaur footprints will be discussed in a subsequent section.

Anchisauripus parallelus (E. Hitchcock)
Figure 3 B

Material. AMNH 1789, a sharp impression of a right pes associated with a footprint of *Apatopus lineatus.* Collected by John Eyerman, evidently in the Smith Clark quarry.

Discussion. In its form and proportions, especially in the slenderness and lack of divergence of digit IV and the relative positions of the articular pads, this specimen is indistinguishable from footprints of *A. parallelus* found in the Portland formation of Massachusetts and Connecticut. Its reconstrueted skeleton corresponds exactly to that of the type specimen as figured by Lull (1953, fig. 42). The Milford footprint, however, is only 6/11 the size of the Massachusetts type. This striking difference in size is associated with no significant difference in proportions: one specimen is a miniature of the other. Despite

our ignorance of trackway characters and range of variation in the Milford form, its form-specific identity is assured.

This is the only footprint species common to the Milford and Connecticut Valley faunules. Whether it represents the same reptilian genus in both areas is of course unknown.

Although no hallux impression is present on the slab, hallux function within populations (or even individual trackways) of *Anchisauripus* is too variable to be of significance in an isolated footprint. Deep creases separate the pads of digits II and III and mark the bases of the strongly flexed lateral claws. Evidently the foot of this dinosaur was rather flexible — perhaps prehensile — at least more so than those of *A. milfordensis* and *Grallator sulcatus*. The fourth digit of *A. parallelus* is longer but clearly less robust than the second, and (at least in the Milford form) appears to be closely joined to the strong third digit. In this respect *A. parallelus* differs from *A. milfordensis*, in which the lateral digits are about equal in robustness and in independence of the third, and differs even more from *G. sulcatus*, in which the second and third digits are joined and the fourth exceptionally independent. The adaptive significance and evolution of these structural patterns can, unfortunately, only be surmised until stratigraphic sequences have been established and skeletal material is available.

GENUS INCERTUM
Figure 4 D

A fourth and most peculiar form of dinosaur is represented by a single small, deep imprint of a left pes, MCZ 214. This footprint might be dismissed as an anomaly of impression if a similar specimen had not been found by Wanner (1889) in the Gettysburg shale of York County, Pennsylvania. Wanner's drawing is reproduced as Figure 4 E; the loss of his original at the U. S. National Museum precludes further comparison.

This animal had a broad, compact foot with the central digit projecting only a toe-width beyond the lateral ones. The imprint is deepest on the lateral side (where it is obscured by worm burrows) and in the free lengths of the second and third digits; the rest of the broad "sole" is two to three millimeters shallower. Little rotational or lateral slippage seems to have

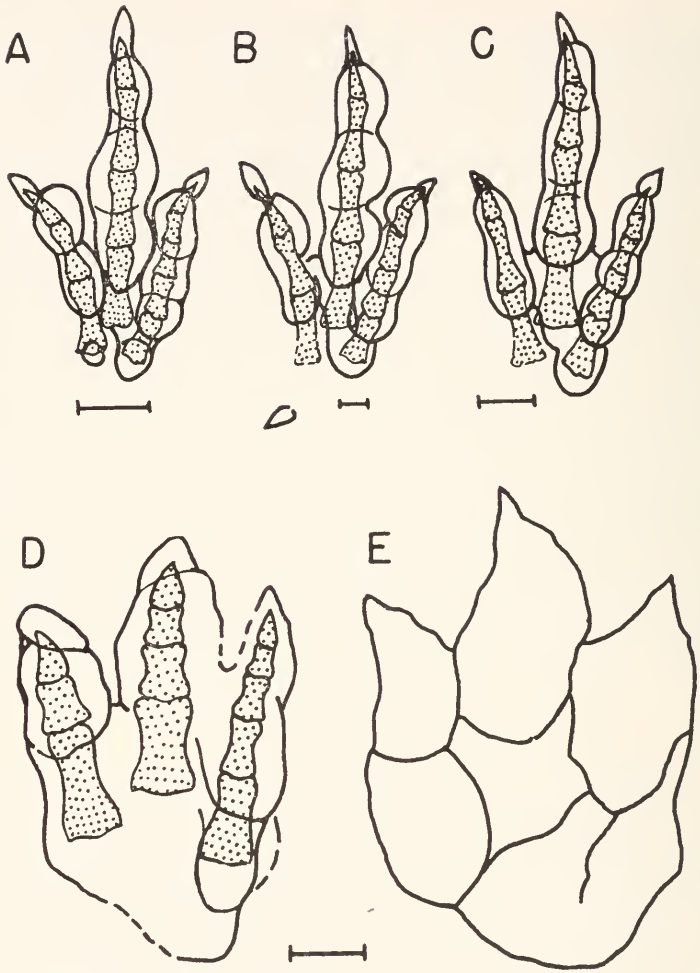


Fig. 4. **A-C,** three dinosaur footprints drawn to common size and orientation, with phalanges restored. **A.** So-called *Grallator gracilis* C. H. Hitchcock, Dartmouth 5023. **B.** Type of *Anchisauripus hitchcocki* Lull, Amherst 56/1. **C.** Plesiotype of *Grallator tenuis* E. Hitchcock, Amherst 17/4. **B** and **C** from Lull. One centimeter scale.

D. Tentative reconstruction of genus incertum from Milford, MCZ 214, x 1. **E.** Similar footprint from Goldsboro, Pennsylvania, x 1 (from Wanner). Apparent sharpness of claw tips may be caused by shrinkage cracks.

occurred: the peculiar proportions of the foot are real. But the material available is insufficient for proper analysis and certainly inadequate for taxonomic treatment.

TAXONOMY OF THEROPOD FOOTPRINTS

Up to this point we have assigned dinosaur footprints from the Delaware Valley to genera best represented in the Connecticut Valley, employing a necessarily typological classification based on similarities and differences in footprint form. This is the traditional approach pioneered by Edward Hitchcock in his "Ornithichnology" of 1836. In Hitchcock's subsequent papers an increasing number of form-taxa were variously grouped and regrouped, with unfortunate wholesale renaming of many units. In this century Lull has achieved a logical taxonomic and nomenclatural reorganization of the Connecticut Valley footprints, a classification which is crystallized in his recent revision (1953).

The three determinable species of theropod footprints from Milford are here assigned to two New England genera which Lull has made the types of two families. Lull's family diagnoses are not, however, mutually exclusive:

GRALLATORIDAE: typically small, footprint tridactyl, limbs very long; with or without tail trace.

ANCHISAURIPODIDAE: bipedal, tetradactyl; hallux when impressed rotated to the rear; well marked phalangeal pads; anterior claws acuminate but not strongly raptorial; no caudal impression.

In current practice *Grallator* is distinguished from *Anchisauripus* "by greater relative length of stride, smallness of track, and the absence of a hallux impression" (Lull, 1953, p. 153). Within each genus the smaller species are distinguished by size, relative length of digits and of stride, and divarication of the lateral digits. But intermediate forms are common, and isolated or incomplete footprints may be difficult to assign to genus and species even when they are clearly impressed.

Let us examine a specific example of close resemblance. A trackway identified by C. H. Hitchcock as his *Grallator gracilis* (Dartmouth 5023) and the type specimen of *Anchisauripus hitchcocki* Lull (Amherst 56/1) are morphologically so similar

that the differences between them fall within the range of individual variation. Lull's plesiotype of *Grallator tenuis* E. Hitchcock (Amherst 17/4) differs from them chiefly in having digit III slightly farther in advance of the lateral toes (see Figure 4 A-C). All are from the Portland formation of the Turners Falls area, Massachusetts. Their differences in size, gait, and incidence of hallux impression are tabulated below. (Data on the Amherst specimens from Lull.)

	"G. gracilis" Dartmouth 5023	*A. hitchcocki* Amherst 56/1	*G. tenuis* Amherst 17/4
Pes length, mm.	51	119	73
Pace length	299	360 to 500	195
Pes: pace length	1:5.9	av. 1:3.6	1:2.7 (1:3.3 in type)
Hallux imprint	absent (?)	present	absent

What do these differences mean? Size difference may be genetic or ontogenetic. Biometric analyses of true populations of Connecticut Valley footprints have not yet been made, but useful series of measurements from footprints of varied ages and sources have been compiled by Lull (1953). In general, dimensions in each species tend to cluster about a mean, with "occasional gradational footprints which bridge the dimensional gaps between the species." This has been interpreted as evidence of several species of reptiles; but as Lull observes, differences caused by sexual dimetry or by selective representation of age groups (perhaps caused by seasonal migration) are difficult if not impossible to evaluate.

The presence or absence of a hallux imprint appears to be a valid distinction in the huge, broad-soled dinosaur tracks of the Connecticut Valley: in *Eubrontes* the hallux is almost never in evidence, while in *Gigandipus* it usually impresses its entire length. In the *Grallator-Anchisauripus* group, however, the distinction is less clear. Rarely does more than the tip of the hallux claw impress, and even this may be totally absent, as in a four-imprint trackway of *A. sillimani* from Turners Falls (MCZ 252, ex Dartmouth 14, cited in Grier, 1927). In current taxonomic practice the absence of a hallux impression does not debar a specimen from *Anchisauripus* but the presence of one debars it from *Grallator*.

This distinction is unconvincing, especially when we consider that the hallux imprint is typically absent in the smaller and present in the larger members of a morphologically homogeneous series. The foot of a large individual bears relatively more weight than that of a small one, as body bulk is proportional to the cube of the linear dimensions: in walking this greater weight on the metatarsus might well cause the pendant hallux claw to impress more frequently. Similarly, a juvenile dinosaur might be expected to take a relatively longer stride than its more ponderous parent. For these reasons it seem unrealistic to maintain generic, much less familial, distinctions between dinosaur footprint species solely on the basis of such largely extramorphologic characters as size, incidence of hallux imprint, and length of stride.

I submit that the characters most diagnostic for the classification of footprints as such, as well as most useful for comparison with skeletal remains, are those which reflect the bony structure of the foot. In most adequately-known varieties of dinosaur footprints the presence of articular swellings and pads permits a reasonably accurate analysis of the skeletal pattern.

To clarify the relationships of the Milford species, therefore, let us compare their restored pedal skeletons with those of other Upper Triassic theropod tracks. For this purpose we must add the phalanges to published figures of the various species, extrapolating to find the length of phalanx III-1 where the position of its proximal end is not indicated by a pad. Because of possible errors in the interpretation of joint position in published figures, this analysis should be considered provisional.

When the skeletons thus reconstructed are compared, the main differences between them are seen to lie in (1) the relative positions of the metatarso-phalangeal joints;[1] (2, 3) the projection of the central digit beyond the lateral ones; and (4) whether digit II or IV projects farther forward. These factors are of course to some extent interrelated. They are more specifically keyed out below, and their distribution among a number of footprint species is shown in Table 2.

[1] This character, the most useful for classification and for skeletal correlations, is also the most difficult to determine in published drawings and faintly-impressed tracks. Close analysis of original material will doubtless necessitate refinements in the subdivision attempted below.

This method of analysis parallels in part the highly instructive comparisons by means of Cartesian diagrams which Lull has appended to his 1953 monograph. (The new insights provided by these diagrams have not, curiously enough, caused Lull to modify his classification of 1915.) My approach, however, concentrates on differences in presumed skeletal structure. By comparing the species of several genera on a single objective basis, rather than matching the previously assigned species of each genus against the type species, it brings out striking inter-generic similarities which might otherwise be overlooked.

DIAGNOSTIC CHARACTERS

1. A. Metatarso-phalangeal joint III about opposite waist of phalanx II-1 and joint 1-2 of IV.
   B. Metatarso-phalangeal joint III about opposite proximal end of II-1 and waist of IV-1.
   C. Metatarso-phalangeal joint III about opposite that of II and joint 1-2 of IV.
2. A. Joint of ungual II about opposite joint 1-2 of III.
   B. Joint of ungual II about opposite waist of III-2.
   C. Joint of ungual II about opposite joint 2-3 of III.
3. A. Joint 1-2 of III about opposite joint of ungual IV.
   B. Joint 1-2 of III about opposite joint 3-4 of IV.
   C. Joint 1-2 of III about opposite joint 2-3 of IV.
4. A. Digit II projects farther anterior than IV.
   B. Digits II and IV project about equally far.
   C. Digit IV projects farther anterior than II.

Let us now attempt a generic regrouping of these species:

I. GRALLATOR, type species *G. cursorius*. *G. sulcatus* clearly belongs to this group despite its atypical forward-set central digit and subequally projecting lateral digits. *G. tenuis* appears to be intermediate between groups I and II, resembling the latter especially in the relative positions of the metatarso-phalangeal joints. A surprise here is that *Otouphepus minor*, though superficially similar to *O. magnificus*, is otherwise quite unlike it and shows itself to be a *Grallator* in size and morphology. This species, based on a single isolated footprint, is of questionable validity.[2] *G. formosus*, included doubtfully by Lull because of its long stride and lack of a hallux imprint, belongs rather to Group III.

[2] The nature of *Otouphepus* is discussed in Appendix 1.

TABLE 2: COMPARISON OF SOME UPPER TRIASSIC THEROPOD FOOTPRINTS

		1.	2.	3.	4.
GROUP I	Grallator cursorius	A	A-B	B	A
	G. cuneatus	A	A	B	A
	G. gracilis[3]	A	A	B	?
	Otouphepus minor	A	A	B	B
	G. sulcatus (Figure 1)	A	A	A	B
	G. tenuis (Figure 4 C)	B	A-B	B	B
GROUP II	Anchisauripus sillimani	B	B	B	A
	"A. exsertus" plesiotype, Amherst 54/1	B	B	B	A
	A. hitchcocki (Figure 4 B)	B	A-B	B	B
	Dartmouth 5023 (Figure 4 A)	B	A-B	B	B
GROUP III	Anchisauripus tuberosus	B	A-B	C	C
	A. exsertus	B	B	C	C
	A. parallelus (Figure 3 B)	B	B	C	C
	A. australis (Argentina)	B	B	C	C
	Jeholosauripus ssatoi (Manchuria)	B	B	C	B-C
	Grallator formosus	B	A-B	C	C
	Otouphepus magnificus	?B	B	B-C	B
	A. minusculus	B	A-B	C	B
	A. milfordensis (Figure 3 A)	B	A	B-C	B
	Eubrontes giganteus	B	B	C	B
	Gigandipus caudatus	C	C	B	A

II. ANCHISAURIPUS (sensu stricto). *A. sillimani,* the type species, shows closest affinities with *A. hitchcocki, G. tenuis,* and the Dartmouth trackway assigned to *G. gracilis.* Amherst specimen 54/1, figured by Lull (1904, fig. 7; 1915, fig. 41; 1953, pl. 10, fig. 11 — but not fig. 41 which is mis-captioned Amherst 54/1 but actually shows 16/6, the type) as *Anchisauripus exsertus* proves instead to be a large *A. sillimani.* (The same is true of Amherst 34/14 in Lull's pl. 10, fig. 12.) Much original material of these forms must be compared before taxonomic decisions can be reached.

[3] Lull's figure of the *G. gracilis* plesiotype appears rather different from C. H. Hitchcock's original figure of the type (in E. Hitchcock, 1865, pl. 9, fig. 7). Perhaps the latter figure is inaccurate or the plesiotype is misassigned.

III. Anchisauripus (sensu lato). Quite a distinct aspect is shown by the larger species of *Anchisauripus* (earlier assigned to *Brontozoum*), in which digit IV is set well forward. Within this group *A. tuberosus, A. exsertus* and *A. parallelus* are so similar that they might be considered a single variable species. *A. australis* Lull (1942) from the Pagazano beds of Argentina is a typical representative of the group. *Jeholosauripus ssatoi* from the "Eo-Mesozoic" of Manchuria (Shikama, 1942) clearly belongs here, as do *Grallator formosus* and *Otouphepus magnificus*. Suppression of the latter genus and species (Baird, 1956; see Appendix I) will remove them from consideration. *A. minusculus* is, as Lull notes, a sharply defined species; it seems to be intermediate between the other members of this group and *Eubrontes giganteus*. *A. milfordensis* is also somewhat transitional but is referred to Group III because of its forward-set central digit and its small size.

Strict consistency would require that Group III be distinguished as a separate genus of the Grallatoridae. Unfortunately there is no Hitchcockian name available for these forms,[4] and rather than make major nomenclatural changes on the basis of this preliminary survey, I will for the present follow Lull's terminology.

The dinosaurian footprint associated with *Chirotherium lulli* at Milford (Baird, 1954, fig. 2 C) and the specimen from York County, Pennsylvania, which Hickok and Willard (1933, fig. 6 B) assigned to *Anchisauripus sillimani* are so different from the forms in Table 2 (and from the Anomoepodidae as well) in the position of their lateral digits that they cannot be classified in the key used here. They apparently belong to a distinct family, which is represented in Europe by *Coelurosaurichnus* (sensu stricto: see Baird, 1954, p. 182). This family is apparently not represented in the Meriden and Portland formations of the Connecticut Valley.

[4] The appropriate and previously used name *Brontozoum* is excluded by nomenclatural technicalities which are discussed in Appendix II.

Order THECODONTIA

Suborder PSEUDOSUCHIA

Form-family CHIROTHERIIDAE Abel, 1935

Genus CHIROTHERIUM Kaup, 1835

Brachychirotherian Group

Diagnosis. Specialized Upper Triassic chirotheriids lacking a thumb-like fifth phalangeal segment distinct from the metatarso-phalangeal pad.

Chirotherium parvum (C. H. Hitchcock), 1889

Figures 5, 6 A; Plate 1, figure 2.

Otozoum parvum C. H. Hitchcock, 1889, pp. 122, 123, 127.
Otozoum parvum. Lesley, J. P., 1889, pp. 571-573, 3 figs.
Otozoum parvum. Lyman, B. S., 1894, p. 214; 1895, pl. 608, figs. 1-3.
?*Otozoum parvum.* Lull, R. S., 1904, p. 515.
?*Chirotherium parvum.* Lull, R. S., 1915, p. 226, fig. 77.
Cheirotherium (?) *parvum.* Lull, R. S., 1917, p. 119.
Chirotherium parvum. Peabody, F. E., 1948, p. 346.
Chirotherium parvum. Bock, W., 1952, pp. 410-414; pl. 41 with plate title 42; pl. 42 with plate title 41; pl. 43, fig. 2 (for Paratype No. S488 read Holotype No. S490).
Chirotherium copei Bock, 1952, pp. 414-415; pl. 43, fig. 1 (for x 1 . . . No. S491 read x 1/2 . . . ANS 15210).
Chirotherium [*copei*]. Richards, H. G., 1953, fig. 176.
Chirotherium parvum, C. copei. Baird, D., 1954, pp. 174, 175.

Type. LC S490, designated by Bock, a large right manus-pes set; the missing posterior half of metatarso-phalangeal pad V is preserved on MCZ 212.

Hypodigm. The type, LC S488 and MCZ 211 probably represent two individuals of similar size. ANS 15210 (type of *C. copei*), MCZ 209, MCZ 210 and AMNH 2257 appear to represent one individual. Horizon, locality and collector as for *Anchisauripus milfordensis* (collector of ANS 15210 is unknown).

Diagnosis. Phalanges of pes digit V reduced and included in the metatarso-phalangeal pad; pes digits IV and V clawless; narrow, curved claws on pes digits I to III borne high above the thickly padded plantar surface and divergent laterally; metatarso-phalangeal pads III and IV coalesced.

History. The type of this remarkable species has been validly designated by Bock, yet curiously enough this may not be the primary specimen on which Hitchcock's species concept was based. The original description, fragmented between two sections of a notoriously imprecise paper, designated no type and was not illustrated. Outline figures of the species, however, appeared the same year in Lesley's hodgepodge "Dictionary of Fossils" with this notation:

> "**Otozoum parvum,** n. sp. C. H. Hitchcock. Fig. 1, hind foot track; fig. 2, fore foot track (both *natural size*); fig. 3, reduction of the two foot prints to show in what relation they stand to each other on the slab of *Trias* sandstone in the quarries at Milford, on the New Jersey side of the Delaware river, about thirty miles above Trenton. Discovered and traced in outline by Prof. C. H. Hitchcock. (See MS. letter, Dec. 1888.) *Upper Trias.* — NOTE. When first seen it was thought to be a *Cheirotherium* track, but it has only four toe marks on each foot." (Lesley, 1889, pp. 571-572.)

These figures, though reprinted by Lyman (*loc. cit.*), have hitherto escaped the attention of bibliographers and researchers alike.

A second outline drawing by Hitchcock, first published in 1915 by Lull, is not identical with the first. Both, however, show the cast of a right manus-pes set, and they are so similar in proportions and particularly in the relative positions of the manus and pes (seldom duplicated exactly in a chirotheriid trackway) that both probably represent the same specimen.

Only one of the existing specimens, the type of *C. copei* Bock, closely resembles these drawings in the features cited. Hitchcock's statement that the pes "is 5 inches long besides 2½ inches of heel" applies to this specimen but cannot refer to the Lafayette College types. Now the early history of the *C. copei* slab, which Bock obtained (mislabeled as to locality) from the effects of an amateur collector of fossils, is obscure; yet the internal evidence indicates that this specimen or one remarkably like it constituted the undesignated, conceptual type of Hitchcock's species. Thus *Chirotherium copei* may be an objective as well as a subjective junior synonym of *C. parvum.*

Variation. The three individuals (or so) represented in the population show a good deal of variation and (if the isolated

tracks are correctly assigned) some intra-individual variation as well. These irregularities are, of course, in addition to those caused by differences in impression and preservation. The type and paratype may represent the left and right feet of the same individual. Pes digit I of the type, however, is relatively longer: its claw-mark extends nearly to the tip of digit II instead of to

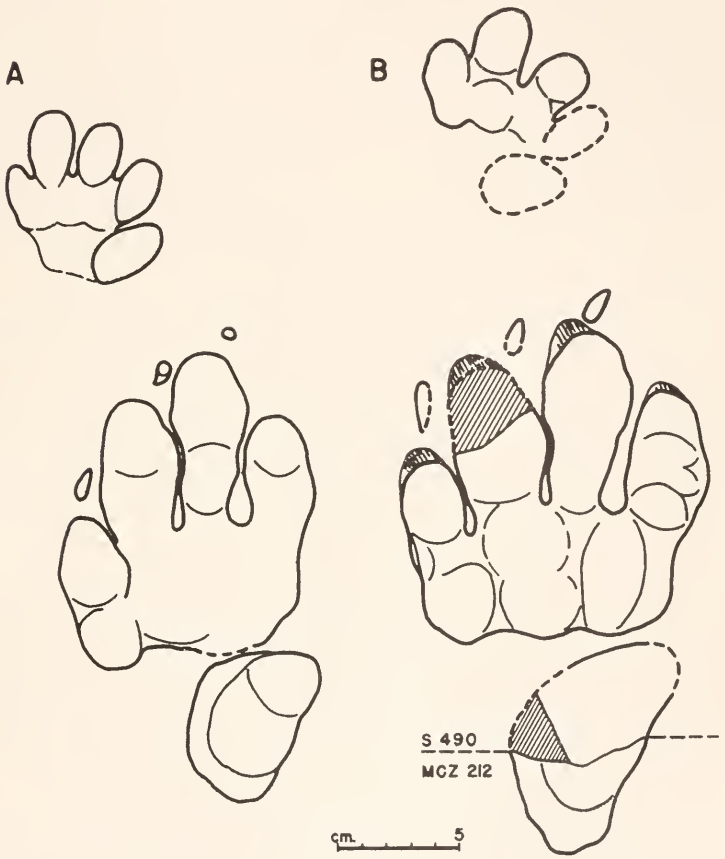


Fig. 5. *Chirotherium parvum* (C. H. Hitchcock), right manus-pes sets, x 1/3. **A.** Type of *C. copei*, ANS 15210. **B.** Type of *C. parvum*, S490 + MCZ 212, showing striated digit-tip impressions.

the base of the distal pad on II, as in S488, MCZ 210, and ANS 15210. MCZ 209 is intermediate in the length of digit I but is otherwise nearly a mirror image of ANS 15210. In relative width of the digit I-IV group and in robustness of manus digit I the type and paratype resemble each other and differ from the smaller, slenderer specimens which are referred to the *"C. copei"* individual (cf. Figure 5).

In my opinion these differences are insufficient to distinguish two species. Individual, age, and sexual variation are to be expected in the Milford reptile population. Differences observed within the hypodigm are minor and do not appear to be correlated. All the specimens exhibit a syndrome of specializations which is unique within the form-genus *Chirotherium* and almost certainly represents a single reptilian genus. Sympatric species of this unusual genus are of course possible, but since similarities greatly outweigh differences, the burden of proof would seem to lie with the splitter.

Morphology. Most of the salient features of this species have been described by Lull and Bock. Curiously enough the pes claws, which are present in every specimen and constitute one of the most distinctive features of the species, remain undescribed and their existence has only been surmised (Bock, 1952, p. 412). These claws were carried high above the plantar surface so that only their tips ordinarily impressed. Spalling of the natural casts obscures the relationships, but where measurements can be made the base of the claw lies at least 6 mm. above the sole of the digit tip.

Instead of forming a linear extension of the digit these claws are turned strongly outward, so much so that the first and second must have nearly touched the sides of the digits lateral to them. The claws were carried in the normal vertical position; their lateral divergence of some 35° seems to be the effect of an oblique ungual articulation, for the digits themselves are otherwise nearly straight.

Claw I is long and narrow and slightly curved laterally; its distal half forms a convex ventral keel rather than a point. Claw II, the heaviest, is carinate along its concave ventral profile but ends in a conical point, sometimes blunted by wear. Claw III is similarly curved and pointed. Of course the depth of the claw-tip impressions has been exaggerated when the toes dug in at

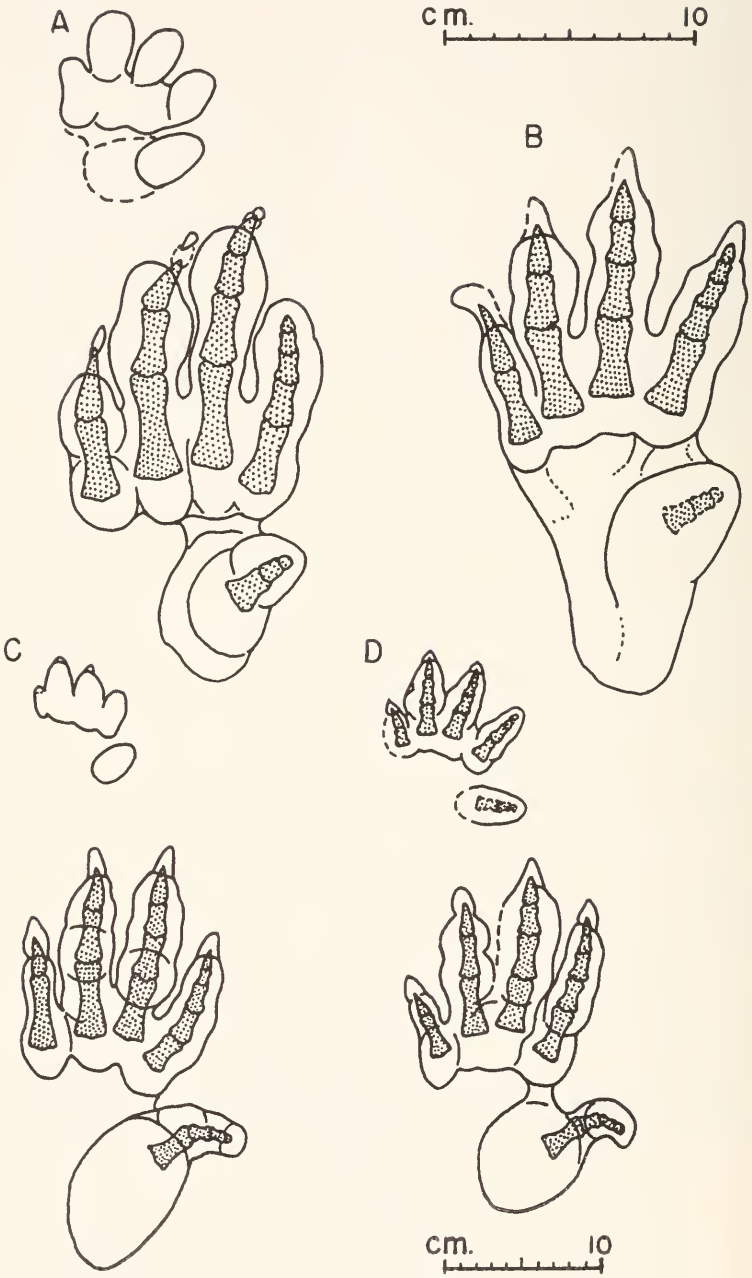
the end of the propulsive phase. Digit IV appears to be clawless in all five specimens, even where the digit-tip impression is 8 mm. deep — an anomalous condition, for a well-developed claw IV characterizes most other chirotheriids.

The vestigial fifth pes digit, so different from the well-developed "thumb" of most chirotheriids, is a striking feature of *Chirotherium parvum*. A single ovoid pad underlies the phalanges and the metatarso-phalangeal joint. As in several other Keuper species (Baird, 1954, p. 174) this pad has migrated somewhat medially from the primitive position, so that the distal end of metatarsal V must have underlain the shaft of IV. Only slight marginal indentations and a suggestion of separate plantar thickenings distinguish the phalangeal section of the pad, which is scarcely longer than its width and narrows abruptly to an ogival, clawless tip.

Almost as distinctive as this digital "heel" is the pattern of plantar pads underlying the metatarsal cross-axis. The metatarso-phalangeal pads form a straight line of low bosses across the posterior edge of the sole; a single flat, subcircular pad underlies the bases of digits III and IV. This condition is quite unusual among chirotheriids. A pad common to two digits occurs in both large-manus and small-manus species but this pad is always central, joining the bases of digits II and III, while the pads of I and IV are distinct. Only in *Otozoum* do we find a single pad for digits III and IV.

Unlike the pes, the manus is typically chirotherioid in form and shows little specialization except that claws are apparently absent and digit V is only slightly offset. (Digits IV and V are definitely clawless but evidence on the others is inconclusive.) The fifth digit is not small and abortive, as Bock terms it, but normal in length and robustness. In the exceptionally deep paratype imprint, moreover, its pad is revealed as merely the slenderer distal part of a large ovoid "heel" which extends postero-medially to a point in line with the axis of digit I. (See Bock, 1952, plate 41 with plate title 42.)

The imprint made by this "heel" pad is 13 mm. deep and slightly undercut laterally. Its steep posterior and postero-medial margins are in strong contrast to the gently sloping margins of the pedal "heel" and suggest that the fifth metacarpal


A
cm. 10
B
C
D
cm. 10

was held nearly vertical as the manus was implanted. The other metatarsals apparently sloped less steeply than the fifth but considerably more steeply than the metatarsal bundle. This evidence of a more digitigrade manus supports the correlation of *Chirotherium parvum* with a reptile of bipedal ancestry in which the forelimbs were shorter than the hind, and in which such a functional lengthening of the forelimb pendulum would have made for more efficient quadrupedal locomotion.

The paratype manus imprint is divided by a large shrinkage crack which, oddly enough, does not exaggerate its width but rather compresses it laterally so that the third and fourth digit impressions are coalesced. The type imprint of *Anchisauripus milfordensis* is also compressed where it is crossed transversely by the same crack. My explanation for this phenomenon is that the shrinkage crack antedated the footprints (see Soergel, 1925, figs. 45-48 for other examples). Before the sand which now forms the natural casts was washed over the recording surface the clay was flooded and consequently expanded, narrowing the shrinkage cracks and thus compressing the footprints. Ichnologist, take warning: things are not necessarily what they seem.

Chirotherium eyermani Baird, n. sp.
Figure 6 B; Plate 2

Eyerman's chirotherium. Baird, 1954, pp. 174, 175-176.

Type. MCZ 134, an isolated left pes imprint collected by John Eyerman in 1887; the only known specimen. Horizon and locality as for *Anchisauripus milfordensis.*

Diagnosis. A moderately large species with slender digit I, short, robust pes digits II-IV bearing heavy claws at sole level, and greatly shortened, hoof-like digit V enclosed in a single pad. Digit IV shorter than II. Metatarsal cross-axis oblique; plantar padding undifferentiated. Manus and trackway unknown.

Fig. 6. Brachychirotherian (**A, B**), small-manus (**C**), and large-manus (**D**) chirotheriids with attempted skeletal restorations. **A.** *C. parvum,* composite of entire hypodigm. **B.** *C. eyermani* n. sp., type (MCZ 134). **C.** *C. lomasi,* Keuper of Storeton, Cheshire (Yale Peabody Museum 3762, a small individual). **D.** *C. barthii,* Moenkopi of Cameron, Arizona (University of California Museum of Paleontology 37315). **A-C** x 1/3, **D** x 1/5.

Morphology. The single footprint of this species, which is impressed to a maximum depth of 40 mm. below ground level, illustrates a fact often overlooked: a footprint is not a cast of the underside of a foot but a composite record of the foot in motion. The effects of structure, function, and preservation are combined in the specimen and must be separated by analysis. If we eliminate the functional distortions of the imprint (which are revealed by slippage marks and variously inclined groups of striations produced by the claws and scales) the foot itself appears to have the form shown in Figure 6 B.

A tendency toward functional tridactyly is evidenced by a strengthening of the three central digits at the expense of the first and fifth. Indeed, the soft mud was resistant enough to bend the feeble first digit upward at a 20° angle to the second. The inward-turned imprint of claw I may be atypical, for such a deflection occurs sporadically in chirotheriid trackways. The undulant outlines and almost undifferentiated pads of digits II-IV are reminiscent of *C. parvum*, but in strong contrast are the straight, massive claws with their slightly convex soles forming an unbroken continuation of the general plantar surface. Also distinctive is the shorter, more divaricate digit I-IV group with its more oblique metatarsal cross-axis and flat, subrectangular sole. From the bases of digits I and IV a pair of ridges which appear to represent the *flexores digitorum breves* extend proximally, converging toward the tarsus. The slope of the longitudinal arch, a feature rarely revealed in chirotheriid footprints, indicates that the first four metatarsals formed an angle of 155° with the proximal phalanges as the pes was implanted.

Digit V, revealed in unusual detail in this footprint, closely resembles that of *C. parvum* except that its phalangeal segment is less pointed and is quite undifferentiated from the metatarsophalangeal pad. This "heel" pad is relatively flat instead of ovoid as in *C. parvum;* it is impressed about 9 mm. deeper than the ventral surface of the longitudinal arch. A definite bridge connecting the "heel" to the base of digit IV suggests a ligamentous connection between the distal ends of the metatarsals. From the sole at the tip of digit V a small falciform web curves upward and joins the side of digit IV, well above its sole.

The distal margin of digit V shows a striation of flutings which average 2.5 mm. between crests. This fluting resembles the striated impressions of claws III and IV and is quite distinct from the scalloped profile produced by fringe scales 3 mm. wide on the medial border of digit II. The greatly reduced fifth digit thus appears to have been tipped with a broad nail or hoof. Such a structure has been reported in no other species of *Chirotherium*.

Osteology of Level B Chirotheriids

The thick, little-differentiated plantar padding in *Chirotherium parvum* and *C. eyermani* makes it impossible to locate all the joints and thus to determine precisely the phalangeal formula. Representative phalangeal patterns may, however, be deduced in other species where articular swellings are well developed. Figure 6 D shows the arrangement in *C. barthii*, the common large-manus species of the European and American Lower (or Middle) Triassic. Here the formula indicated is manus 2-3-4-?4-?3, pes 2-3-4-5-?4. An Upper Triassic member of the same group, *C. lulli*, is basically similar but appears to have only three phalanges in the thumb-like fifth digit (Baird, 1954, fig. 2 A). In the best-known small-manus species, *C. lomasi* of the English Keuper (Figure 6 C), a formula of 2-3-4-5-?4 is evident in the pes but no skeletal pattern is discernible in the hoof-like manus.

In preparing the skeletal restorations of *C. parvum* and *C. eyermani* I have indicated joints at localized thickenings in the sole wherever possible, and have extrapolated as little as possible from the structure of other species. In *C. parvum* a slight differentiation in the coalesced pad of pes digit V suggests the presence of three phalanges, so by analogy the same number is hypothesized for *C. eyermani*.

Classification of Chirotheriids

Peabody, working chiefly with Lower Triassic species, has separated the better-known chirotheriids into a typical or large-manus group and a specialized small-manus group. Ratios of manus to pes area in representative members of each group are

tabulated below, in order of decreasing relative manus size. (Areas include only the digits and metapodio-phalangeal pads. These ratios, based on single manus-pes sets, are not necessarily typical of the species listed.)

Large-Manus		Small-Manus	
C. lulli Bock	1:2	*C. coltoni* Peabody	1:5.7
C. storetonense Morton	ca. 1:3	*C. marshalli* Peabody	1:5.7
		C. lomasi Baird	1:6.6
C. minus Sickler	1:3		
C. wondrai Heller	1:3.4		
C. barthii Kaup	1:3.6		

In *Chirotherium parvum* the type manus is too incomplete for areal measurement but ANS 15210 furnishes reliable figures of 25 cm.^{2} for the manus and 112 cm.^{2} for the pes. (Bock's measurement of 85 cm.^{2} for the pes apparently omits the "thumb" pad.) The resulting manus-pes ratio of 1:4.6 falls between the ranges of the two groups. Except for the closeness of digit V to its fellows the manus of *C. parvum* is more similar to that of the large-manus species than to the compact, hoof-like forefoot of the small-manus group. Unfortunately, nothing is known of the manus in *C. eyermani.*

The shortening of pes digit IV, moderate in *C. eyermani* but extreme in *C. parvum*, would seem on typological grounds to ally these species with the small-manus group, in which such a shortening is characteristic. In terms of function, however, this condition is obviously essential to the maintenance of symmetry in any walking foot in which the fifth digit has undergone reduction. Other examples are found in the feet of dinosaurs, crocodiles and birds (where apparent exceptions such as *Gavia, Pelecanus* and *Hesperornis* prove the rule, since walking is not the primary function of the foot). Thus the shortened fourth digit in the Milford species is functionally correlated with the vestigial fifth digit and indicates parallelism rather than affinity with the small-manus group.

The Level B chirotheriids thus appear to represent a lineage distinct from the small-manus group although paralleling it in adaptive modifications and similarly derived from a primitive large-manus stock. This lineage has been progressively modified

to a point where it must be considered a distinct sub-generic group, characterized by the short, oval, heel-like fifth pes digit.

This group, here recognized in North America for the first time, is represented by specimens from several horizons in the Middle Keuper of Germany (Heller, 1952). The oldest of these, an imperfect pes imprint from the Blasensandstein of Franken, was described by O. Kuhn (1936) as *Chirotherium* sp. In size and proportions it shows a decided resemblance to the Level B species, particularly *C. eyermani,* differing chiefly in the greater length of digit V.

A rather similar but slightly younger form is *Chirotherium thuringiacum* Rühle von Lilienstern (1938) from the Plattensandstein (km 4 zeta) of Thüringen. This species recalls *C. eyermani* in its short, divergent pes digit I-IV group. It resembles *C. parvum* in its round, apparently clawless digit tips; and the manus with its plump, clawless toes and close-set, medially shifted digit V is strikingly similar.

Slightly higher in the Middle Keuper, in the Semionoten-Sandstein of Franken, occurs a group of chirotherioid footprints which Beurlen (1950) has named *Brachychirotherium hassfurtense.* Though the specimens figured are somewhat heterogeneous they all show a foot structure like that described above, with apparently clawless digits and an abbreviated "thumb." The latter appears so inconsistent in its size, position, and orientation, and the relative lengths of the other digits are so variable from specimen to specimen, that definitive diagnosis of the species (singular or plural) is impossible. Unfortunately, all these German forms have been described from individual footprints rather than analyzed on the basis of a composite of each population. Specific distinctions are by no means clear, particularly as no types have been designated, and the differences carefully tabulated by Heller may or may not be significant. Nevertheless these Middle Keuper species from Germany are clearly referable to the same group as *C. parvum* and *C. eyermani.*

For this group Beurlen has established the separate genus *Brachychirotherium.* Since the differences between this and the large-manus group are little greater than those which distinguish the small-manus group from both, I prefer to broaden slightly the scope of the form-genus *Chirotherium* to include a third

sub-generic group for which Beurlen's name may appropriately be retained. Following the example of Peabody I assign this group no formal Linnaean status.

Evolutionary Tendencies

The modifications seen in this brachychirotherian group are clearly consistent with the general evolutionary trend of Keuper chirotheriids which I have previously outlined (1954, p. 188): the tendency of an osteologically pentadactyl stock to become functionally tetradactyl through elimination of the lateral propping function of the fifth pes digit. In the brachychirotherian group this was being accomplished by several means: by shifting the distal end of the unshortened metatarsal V more or less medially, beneath and behind the shaft of metatarsal IV; by progressively shortening and straightening the fifth digit to minimize its lateral projection; and ultimately by incorporating the metatarsal and phalanges into a single, inflexible heel structure. During this process a gradual shortening of digit IV tended to maintain the symmetry of the foot. Concomitantly the manus became smaller and more compact.

Although — most unfortunately — we have no trackways from which to determine the locomotor habits of the group, it seems inescapable that these modifications promoted more efficient locomotion, presumably cursorial and (as Rühle von Lilienstern points out) showing bipedal tendencies in some members. Increasing competition from the expanding and diversifying stocks of saurischian dinosaurs may well have channeled chirotherian evolution along these lines.

Changes in foot structure and locomotor pattern are of course only a part of the overall adaptive modification which must have taken place in the brachychirotherian group. Only a part, yes: but surely an important one, for, as I have shown (1954, p. 174), convergent modifications were independently taking place in Keuper representatives of both the large-manus and small-manus groups. Apparently the chirotheriid locomotor equipment of early Triassic time had been found inadequate for the conditions of mid-Keuper life.

The chirotheriid response to changing conditions was, however, insufficient. We have noted that even in the most special-

ized species, *C. parvum* and *C. eyermani,* the once thumb-like fifth digit was still functional in modified form. Dinosaurs and small pseudosuchian or proto-crocodilian types such as *Batrachopus,* in which locomotion had become more efficient through the loss or atrophy of the fifth digit, eventually replaced *Chirotherium.* Huge size and bipedality (along with other specializations yet unknown) permitted a lone descendant of the chirotheriid stock, *Otozoum,* to survive until the close of Newark time — but that is another story.

Osteological Correlations

That chirotheriid trackways are the products of various pseudosuchian reptiles is now generally accepted. Beyond this premise the foregoing discussion has avoided assumptions as to the identity of the Milford trackmakers, attempting instead an objective analysis of the ichnological evidence as such. The possible position of these trackmakers among the Pseudosuchia can now be examined.

At present the pedal skeletons of most Upper Triassic pseudosuchians are too inadequately known to permit useful comparisons with the three Milford species of *Chirotherium.* The relatively conservative large-manus species *C. lulli* has been interpreted as a small, persistently quadrupedal ornithosuchid not too different from the presumably ancestral form *Euparkeria;* but closer comparisons are impossible. Among middle to late Triassic reptiles which might be compared to the brachychirotherian species only two, *Prestosuchus* and *Typothorax,* are represented by even relatively complete foot material.

As restored by Peabody (1948, fig. 39 B-C[5]) the pes of *Prestosuchus* is broad and short-toed, suggesting (as Peabody notes) the brachychirotherian *C. thuringiacum* Rühle. Lack of the tip of digit IV and all phalanges of digit V, however, precludes for the present any correlation of *Prestosuchus* with one or another of the chirotheriids. Certainly the phalanges are relatively much shorter than those restored for the Milford footprints. As Huene (1944) records only a single phalanx from the manus, Pea-

[5] Peabody has followed Huene in reversing the proximal overlap of the metatarsals although the natural relationship is preserved in the specimen itself — cf. Huene, 1944, pl. 20, fig. 4 a-b.

body's very plausible reconstruction of the manus digits cannot be used for comparison.

Despite the strong contrast in habitus between the relatively narrow-bodied, lightly-armored, predaceous *Prestosuchus* and the broad-backed, heavily-armored, necrophagous *Typothorax* (Sawin 1947), the two are strikingly similar in phalangeal pattern. Thus the general aspect of *Typothorax* is brachychirotherian-like but its short phalanges seem to eliminate it from comparison with the Milford footprints. The manus is decidedly chirotherian in form although its fifth digit appears to have been somewhat weaker than that of most chirotheriids. Areas of the digit I-IV groups in manus and pes bear a ratio of about 1 to 3, a ratio found in *C. thuringiacum* and some large-manus chirotheriids. If brachychirotherian trackways were available the pedal similarities between *Prestosuchus* and *Typothorax* should cause little difficulty in correlation, for the swift-striding predator must have left a much narrower trackway than its broad-beamed, ponderous relative. But pending the discovery of such additional evidence the systematic positions of the Level B pseudosuchians must remain uncertain.

Order THECODONTIA

Suborder PHYTOSAURIA

Form-family APATOPODIDAE Baird, nov.

Genus APATOPUS Baird, nov.

Type species *A. lineatus* (Bock), 1952; family and genus monotypic.

Diagnosis. Quadrupedal trackway with pace angulation about 108°, pes but not manus toed-out. Feet pentadactyl with well-developed articular swellings and sharp claws; manus short and symmetrically radiate, pes long and narrow with digits in order of increasing length V-I-II-III-IV.

APATOPUS LINEATUS (Bock)

Figures 7, 8; Plates 3, 4

Otozoum (?) lineatus Bock, 1952, pp. 408-409, pls. 48, fig. 1 and 46, fig. 1 (mistitled "Type No. 15230" for LC S489). Probable earlier syn-

onymy in Table 1; the variety of past assignments suggested the generic name. Diagnostic characters are those of the genus.

Type. LC S490, a left manus-pes set (Bock's type) plus MCZ 212, the succeeding right set of the same trackway.

Hypodigm. The type, S489, and MCZ 213, presumably three adults; AMNH 1789 and 2258, smaller individuals; AMNH 2259 and MCZ 214, juvenile (same individual?). Source data as for *Anchisauripus milfordensis.*

Trackway. By a remarkable and fortunate coincidence a tiny contact area between corners of the Lafayette and Harvard slabs permits the reconstruction of the type trackway. (This contact crosses the "thumb" of the *Chirotherium parvum* type, cf. Figure 5 B.) Trackway parameters determined by direct measurement or by extrapolation (*) are tabulated below. In the first three the reference point is the center of metatarsophalangeal pad III:

Pace, angular	42.5 cm.
Stride	*70 cm.
Pace angulation	*108°
Gleno-acetabular length (approximate)	*52 cm.
Interpes width (between median margins)	13.7 cm.

Pedal morphology. The additional material now available permits analysis which was impossible with the incomplete, obscure, single manus-pes set on which the species was based. A composite restoration derived from all this material is presented in Figure 7. The digits of both manus and pes are shod with domed, oval articular pads separated by slender waists, so that joint positions are apparent in profile as well as in section. The claws are slender and rather crocodilian in the manus but appear heavier and more triangular in the pes, where rotation during withdrawal has obscured their exact form. As the plates show, laterally flexible ungual articulations permitted much lateral movement in both manus and pes claws.

The manus is nearly symmetrical around digit III, the metacarpo-phalangeal pads forming a regular semicircle, so that in form and proportions it recalls the manus of *Mesosaurus* — an aquatic form. A phalangeal formula of 2-3-4-?5-?3 is indicated. In normal function the manus was digitigrade and only in the deepest imprint did the palm register (Plate 4, figure 1).

The pes with its long fourth digit and peculiar sole is quite

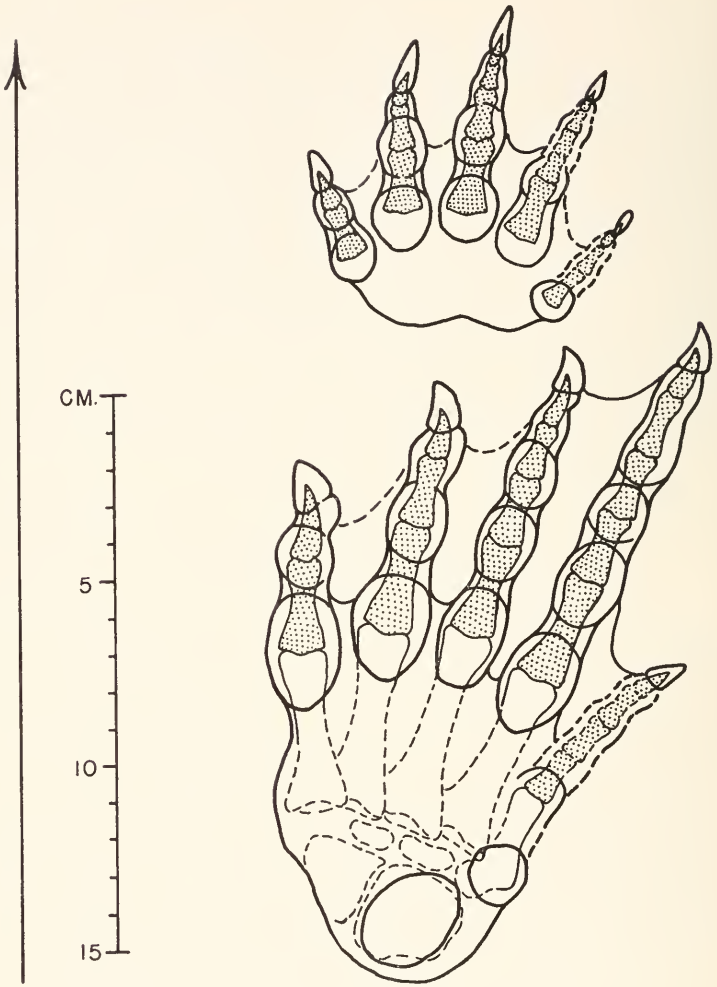


Fig. 7. *Apatopus lineatus* (Bock), composite restoration based on type (8490 + MCZ 212) with parts of digits IV and V restored from other specimens, x 1/2. Arrow represents midline of trackway.

distinct from other Triassic footprint types. At first glance it appears to show affinities with primitive reptilian pedes of the pelycosaur or captorhinomorph type, but the fact that metatarsal IV is slightly shorter than III (rather than the reverse) indicates that digit IV has been secondarily lengthened by hypertrophy of its phalanges. A similar secondary lengthening of the phalanges of digit IV occurs in the manus of the marine turtle *Chelonia mydas* (cf. Abel, 1912, fig. 111). Aquatic adaptation is the most obvious explanation for such a modification, and this interpretation is supported by the evidence of interdigital webs. Although the length and position of the short fifth digit are evident its structural details are obscure; my conjectural restoration shows four phalanges, making the pes formula 2-3-4-5-?4.

The extent of interdigital webbing in *Apatopus* is uncertain, particularly because the pes in walking was often laterally compressed so that web margins would have left no mark. The best-represented web connects the bases of pes claws III and IV, an arrangement quite in contrast to that in living crocodilians, in which the deeply recessed webs occupy only part of the interdigital area. Additional (though circumstantial) evidence for the presence of webbing is the fact that digits IV and V are adequately recorded only in the deepest footprint, which suggests that distribution of the animal's weight over a webbed area effectively reduced the depth of impression. Here as in other fossil footprints, unfortunately, the evidence is less than satisfactory.

Traces of the squamation are preserved only in the juvenile MCZ 214 (Plate 4, figure 1). Here the digits of manus and pes show a fine beaded or pustulose texture which compares closely with the skin of corresponding areas in a juvenile *Gavialis gangeticus*.

Except in the deepest impressions the sole is very indistinctly recorded. Some understanding of it can nevertheless be obtained by collating outlines printed from latex molds of several specimens. On the medial margin a bulge marks the position of the first metatarsal's proximal head, and opposite this is a circular pad which must have underlain the fifth metatarsal. On this basis the first four metatarsals have been restored in normal alignment. Its distinct individual pad suggests that the proximal end of metatarsal V was less elevated than that of metatarsal IV;

if so, then the fifth metatarsal probably articulated with the tarsus by a hooked, dorso-medially directed process. Postero-medial to this area a large, subcircular calcanear pad forms the heel of the footprint. The possible presence of a tuber calcanei is suggested by the relatively deep impression of this pad. Though plausible, this interpretation of the tarso-metatarsal area rests on admittedly tenuous evidence.

Variation. Aside from striking variations in the manner of impression, which are apparent in the plates, the *Apatopus* footprints reveal only minor differences among the six (or so) individuals of the population. Chief of these is size: the smallest individual, AMNH 2259, has a pes length just half that of the type (as restored). Osteological analysis reveals the structural unity of these footprints which might otherwise be assigned to a number of form-species.

Affinities of *Apatopus*

Examination of Triassic footprints from every continent yields nothing similar enough to *Apatopus* to justify comparison in terms of footprint taxonomy. We may more profitably investigate the nature and systematic position of the trackmaker. In its foot structure and body proportions *Apatopus* shows closest affinities to quadrupedal members of the Subclass Archosauria — i.e. the Phytosauria, Pseudosuchia and Crocodilia. These groups will be considered in reverse sequence, beginning with the best known.

Locomotion in crocodiles, which has been investigated by Abel (1912, p. 217), Huene (1913), and Schaeffer (1941, p. 443 ff.), is of three types: a slow, lizard-like dragging of the body, a spring in which all four feet thrust simultaneously, and a striding gait in which the belly is well above the ground and only the tail-tip leaves a mark. Of these gaits only the last would produce trackways comparable to that of *Apatopus;* thus neither the "Gehspur" nor the "Laufspur" which Huene figures is pertinent to this discussion. An example of the true striding gait in a juvenile *Alligator mississipiensis* has been recorded on film by Schaeffer. The resulting trackway shows a pace angulation of only 80°, i.e. the stride is little longer than the pace. In evaluating this record the smallness of the alligator and the

Fig. 8. Type trackway of *Apatopus lineatus* (Bock) with third manus-pes set added and footprints somewhat restored, x 1/6. Lafayette College S490 plus MCZ 212.

fact that it was walking on glass must be considered. For example, the 20° to 30° outward rotation of the pes between implantation and withdrawal can hardly be normal: no such rotation is evident in the alligator trackway figured by Jaeger (1948, pl. 170 c), and only in very muddy footing did the pes of *Apatopus* rotate a few degrees outward (cf. Plate 4, figure 2). I believe that on a fairly firm surface a crocodilian in rapid motion would produce a trackway rather similar in proportions to that of *Apatopus*. We have already noted the crocodilian habitus indicated by the aquatic adaptations in the feet of the Milford trackmaker.

Despite these similarities in habitus *Apatopus* can hardly have been a crocodilian by heritage. The ancestral crocodilian *Protosuchus* from Upper Triassic or Lower Jurassic beds of Arizona had already developed an essentially modern type of foot with an elongate metatarsus, reduced fourth and rudimentary fifth digits, and a formula of 2-3-4-4-0 (Colbert and Mook, 1951). These characteristics were probably inherited without much modification from pseudosuchian ancestors and have been transmitted without much modification to the living crocodilians. Even the aberrant pes structure in the marine thalattosuchians can be more readily derived from the *Protosuchus* pattern than could that of *Apatopus*. Another point of distinction is the outturned manus which characterizes crocodilian trackways. Thus the Milford trackmaker cannot be referred to any crocodilian lineage.

Among trackways which have been ascribed to pseudosuchians certain members of the *Batrachopus* group approach the *Apatopus* pattern. Nevertheless the reconstructed feet of these forms — and the few known pseudosuchian foot skeletons — are distinctly different, particularly in the fourth and fifth pes digits.

In the Phytosauria we find the logical correlative for a trackmaker which is crocodilian in body form and presumed habitus but not in skeletal structure. The comparative proportions of the crocodilians *Gavialis*, *Tomistoma* and *Alligator*, and the phytosaurs *Rutiodon*, *Machaeroprosopus* and *Mystriosuchus* have been analyzed by Colbert (1947), who attests to the remarkable parallelism noted by earlier authors. Very little articulated phytosaurian foot material, unfortunately, is available for comparison with the footprints. The manus is best represented

in *Mystriosuchus* (McGregor, 1906, fig. 10), in which — like *Apatopus* — the metacarpal bundle is nearly bilaterally symmetrical and digit V bears three phalanges which are about twice as long as they are wide. Further comparisons cannot be made. McGregor's reconstruction of the pes in *Rutiodon,* based on incomplete, scattered material of several individuals, is remarkably similar to my restoration of *Apatopus* — which (except where drawn in dashed lines) was quite independently derived from the footprints alone. If *Apatopus* is indeed a phytosaur, then Dr. McGregor proves to have been indeed a prophet worthy of honor.

Correlation with the Phytosauria is supported by all the evidence and contradicted by none; it may therefore be taken as a working assumption. Possible equivalents exist in the two phytosaurs of the Newark series, *Rutiodon* and *Clepsysaurus* (?=*Machaeroprosopus*). The significant differences in skeletal proportions between these genera would presumably be reflected in their trackways and may someday permit positive assignment of *Apatopus lineatus* to one or the other. Present knowledge, however, does not justify comparison of the single, partial *Apatopus* trackway with the composite skeleton of *Rutiodon* from North Carolina (Colbert, 1947) as opposed to incomplete skeletons from Arizona which may be congeneric with *Clepsysaurus* (Camp, 1930). Geographic distribution of the Newark phytosaurs offers a possible guide to the identity of *A. lineatus,* for Colbert and Chaffee (1941) concur with Camp's conclusion that all the phytosaur remains from Pennsylvania, New Jersey, and Connecticut represent *Clepsysaurus* while the North Carolina finds all pertain to *Rutiodon.*[6] *Apatopus lineatus* would thus appear to be a correlative of *Clepsysaurus.*

So far as I know these Milford specimens are the only phytosaur footprints yet described.[7] Paradoxically, phytosaur bones are the commonest skeletal remains of both the Chinle formation of the Southwest and the Newark series of the East (excluding,

[6] H. E. Wanner's (1926) specimens of *"Rutiodon carolinensis"* from the Newark series of York County, Pennsylvania — overlooked by the above-mentioned authors and by the Hay-Camp bibliographies — merit further study.

[7] An isolated pes imprint, considered by Bock (1952, pl. 46, fig. 2) to be probably that of a large parasuchian of the *Clepsysaurus* type, bears no resemblance to *Apatopus.* So far as its preservation permits comparisons, it seems more similar to ornithoid footprints of the *Plectropterna* type from the Connecticut Valley.

significantly, the Meriden and Portland formations). In the ecology lies the probable explanation for this discrepancy: Triassic footprint assemblages as a rule represent terrestrial faunas while the fossil deposits contain a disproportionate number of aquatic forms. Thus the presence of several phytosaurs in a dinosaur-pseudosuchian-lacertoid footprint faunule at Milford is rather anomalous.

REPTILIA LACERTOIDEA INCERTAE SEDIS

Genus RHYNCHOSAUROIDES Beasley *in* Maidwell, 1911

Pontopus Nopcsa, 1923, p. 141. Keuper of England.

Akropus Rühle von Lilienstern, 1939, p. 298. Bunter of Germany; Moenkopi of Arizona (Peabody, 1948, p. 319 ff.).

Hamatopus Rühle von Lilienstern, 1939, p. 319. Bunter of Germany.

Rhynchocephalichnus Huene, 1941, p. 14. Keuper (Verrucano) of Italy; Keuper of Germany (Heller, 1956).

Eurichnus Lull, 1942A, p. 502; Branson, 1947, p. 590. Lower Triassic (Chugwater) of Wyoming.

The type species is here designated as *R. rectipes* Beasley *in* Maidwell, the type specimen of which is a manus-pes set from the Keuper of Daresbury, England (Dr. Ricketts' collection, University of Liverpool Geology Department).

RHYNCHOSAUROIDES HYPERBATES Baird, n. sp.
Figures 9 A, 10

Type. ANS 15210, a trackway of one pes and three manus imprints associated with the type of *Chirotherium "copei."*

Hypodigm. The type; an isolated left pes on the same slab; MCZ 210, a partial left pes associated with *C. parvum.*

Diagnosis. Manus broad with little disparity in digit lengths; gait digitigrade with hallux non-functional and proximal ends of proximal phalanges normally carried clear of the ground. The specific name alludes to the overstepping of manus by pes.

Morphology. The trackway is rather narrow, showing a stride of 44 cm., forelimb paces of 23 and 25.5 cm., and a pace angulation of 130° between manus imprints. (In these measurements a 3-cm. fissure filling which crosses the trackway is ignored, as the relative ages of trackway and fissure are unknown.) As in

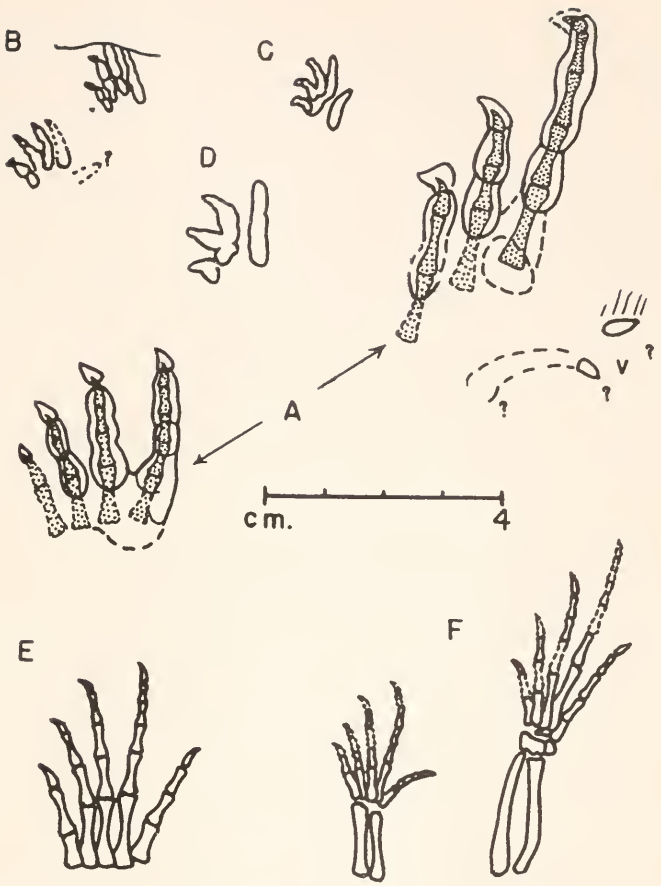


Fig. 9. **A.** *Rhynchosauroides hyperbates* n. sp., composite restoration of manus (at left) and pes in normal position. **B-C.** Small *Rhynchosauroides* footprints from Milford: **B,** (ANS 15210); **C,** manus imprint (MCZ 213). **D.** Manus imprint from Trostle quarry near York Springs, Adams Co., Pa. (Carnegie Museum 12082). **E.** Manus of *Monjurosuchus* reconstructed from Endo's photograph. **F.** Manus and pes of *Polysphenodon mülleri* Jaekel, modified from Huene. All x 4/5.

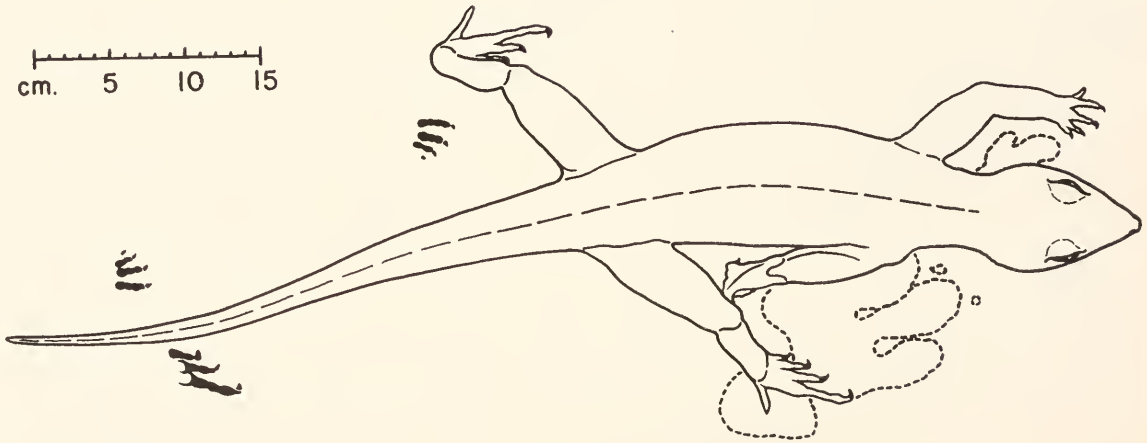


Fig. 10. Type trackway of *Rhynchosauroides hyperbates* n. sp. (ANS 15210), x 1/5, with trackmaker restored as a sphenodontid rhynchocephalian. First manus-pes set and left pes added, fifth digits hypothetical. Footprints of *Chirotherium parvum* (*C. "copei"* type) in dashed outline.

other Triassic lacertoid trackways the pes is strongly out-turned and evidently overstepped the manus as it implanted.[8] The trackmaker, which is restored in walking pose in Figure 10, had a gleno-acetabular length of about 18 cm. and a total length of perhaps 75 cm.

The foot structure, revealed by comparing outlines printed from latex molds of all the imprints, is decidedly lacertoid. Well-developed articular swellings indicate an apparent phalangeal formula of 1-2-3-4-? in the manus and ?-2-3-4-? in the pes. This formula must be incomplete, for the obvious reptilian character of the feet connotes a normal formula of 2-3-4-5-3(4). Like the structurally similar Moenkopi genus *Rotodactylus* (Peabody, 1948, p. 329), the Milford form must have been digitigrade to such an extent that each proximal phalanx was elevated with its metapodial; normally only the padded distal articulation of phalanx 1 touched the ground. All the digits recorded bear sharp claws, either extended or curved toward the trackway midline.

The pollex is represented only by claw impressions. Nothing which can be identified as the imprint of a fifth manus digit is visible. The absence of any hallux imprint and the disparity in length of the pes digits indicate that the hallux was non-functional. Pes digit V has left no unequivocal record, but obscure marks on MCZ 210 and ANS 15210 may have been made by a lacertoid, laterally projecting minimus. Both these marks are shown, for what they may be worth, in Figure 9 A.

Rhynchosauroides sp.

Figure 9 B, C; Plate 3, Figure 2

A pair of minute footprints on the ANS slab, unfortunately too incomplete for reliable analysis, and indistinct trackways of comparable size on a slab with *Apatopus lineatus* (MCZ 213) prove the presence of another species of *Rhynchosauroides* in the Level B faunule. Smaller size and greater disparity in the lengths of the manus digits distinguish it from *R. hyperbates.*

[8] I have seen no evidence in Pennsylvanian, Permian, or Triassic lacertoid trackways that the pes rotated nearly 90° outward during the propulsive phase as Schaeffer (1941, p. 449) has observed in experiments with *Anolis.* Except for an occasional rotational slippage of a few degrees in unusually soft mud the pes remained in implantation position until withdrawn.

Relationships

Lacertoid trackways of this sort are familiar companions of *Chirotherium* in the Lower and Upper Triassic of both Europe and America. As indicated in the synonymy, a number of generic names have been applied to them. The differences between these nominal genera are, however, slight: for example, Rühle von Lilienstern distinguished *Hamatopus* from *Akropus* largely by the more hooked appearance of its digit tips. A more practical treatment here proposed is to consider these forms as species of a single form-genus *Rhynchosauroides* which is comparable to *Chirotherium* in its range of variation. This form-genus, of cosmopolitan distribution in continental Triassic beds, undoubtedly represents several reptilian genera; but until more is known of Triassic lacertoid feet and footprints there seems little advantage in proliferating form-genera on differences of uncertain diagnostic value.

Our lack of data on the fifth digits of manus and pes hinders comparison of *Rhynchosauroides hyperbates* to other species. Its closest similarities, however, are to the footprints from the English Keuper which were described by Beasley (1905) and comprehensively reviewed by Maidwell (1911, 1914). The smaller Milford lacertoid is less similar to the larger one than to *Rhynchosauroides* [*Rhynchocephalichnus*] *franconicus* (Heller, 1956; see also Haarländer, 1938) from the Keuper of Germany.

Such trackways have never been found in the well-known footprint faunas of Portland and Meriden age in the Connecticut valley, though they are not uncommon in the Brunswick and Lockatong formations of the Pennsylvania-New Jersey basin. The Milford forms cannot adequately be compared with *Rhynchosauroides* [*"Orthodactylus"*][9] *howelli* (Bock) from an earlier horizon of the Brunswick near Schwenkville, Pennsylvania, until better-preserved material is available. An isolated *Rhyncho-*

[9] This form has nothing to do with Hitchcock's *Orthodactylus* from the Portland formation of Gill, Massachusetts. The type specimen of the type species *O. floriferus* is an obscurely recorded trackway of pseudosuchian or protocrocodilian type, having the manus anterior to the pes and strongly out-turned as in the contemporary *Cheirotheroides*. Superficial similarity of the digital gouge-marks apparently prompted Bock (1952, p. 421) to refer his Schwenkville tracks and some Lower Permian "Schwimmspuren" (Schmidtgen, 1927, fig. 3) to *Orthodactylus*. On the other hand, Triassic "Schwimmspuren" similar to Schmidtgen's and equally indeterminate were made the type of a new species, *Procolophonipus conhuenei* Bock (p. 419), ascribed to a plump, slow-moving reptile which jumped quadrupedally without leaving manus imprints.

sauroides manus imprint of Brunswick age from the Trostle stone quarry near York Springs, Adams County, Pennsylvania, is shown in Figure 9 D; and another of Lockatong age from Phoenixville, Pennsylvania, has been figured without name by Bock (1952, pl. 48, fig. 2). Aside from some undescribed trackways from the Dockum group of the Cimarron Valley in northeastern New Mexico (AMNH 6338), these are the only records of *Rhynchosauroides* in the Upper Triassic of North America.

The systematic position of the trackmakers is debatable. Footprints of this sort have been referred by various authors to the Protorosauria, Eosuchia, Pseudosuchia, Rhynchocephalia and Lacertilia: and indeed each of these groups has Triassic representatives which would have made lacertoid footprints. Among the Protorosauria the tanystropheid *Macrocnemus* from the Alpine Middle Triassic (Peyer, 1937) is similar in size and proportions. Its reduced fifth digits of manus and pes exclude it from correlation with the European species of *Rhynchosauroides*, and its greater disparity in the lengths of the manus digits distinguishes it from the larger Milford form. A similar disparity characterizes the manus of *Trilophosaurus* from the Upper Triassic (Dockum) of Texas (Gregory, 1945); but its pes digits are much less unequal in length. The proximal end of ungual II lies opposite those of phalanges III-3 and IV-2, while in the footprints it lies opposite the proximal end of III-2 and the waist of IV-1, much as in the Permian *Protorosaurus*. But as the known Triassic protorosaurian genera undoubtedly constitute only a fraction of the number that once lived, the group cannot be disregarded as a possible source of Keuper lacertoid trackways.

Too little is known of limb structure in the Eosuchia to permit useful comparison.

Peabody (1948, p. 337) has referred his Lower Triassic footprint genus *Rotodactylus* to the Pseudosuchia on the basis of its long-striding gait with pendulum limb movement, its semibipedal concentration of the body weight on the long hind limbs, and its digitigrade pes with posteriorly rotated, prop-like fifth digit. Isolated manus-pes sets of *Rotodactylus* appear deceptively lacertoid (especially where the fifth digit has failed to impress), but the whole organization of the animal is significantly

different from that of lizard-like reptiles.[10] Aside from its overstepping gait and similar digitigrade specialization the Milford trackmaker appears to be basically unlike *Rotodactylus.* No comparable pseudosuchian skeleton is known.

The case for the Rhynchocephalia as a source for Triassic lacertoid footprints, reviewed by Huene (1938, 1941) and Peabody (1948), dates historically from Richard Owen, who in 1842 assigned the small footprints of the Grinsill quarries near Shrewsbury to *Rhynchosaurus articeps* on the grounds that the bones and footprints correspond in size and occur in the same beds, to the exclusion of other bones and footprints. This correlation was accepted by subsequent students of British Keuper footprints and indeed motivated Beasley to coin the name *Rhynchosauroides.*

A basic similarity certainly exists between *Rhynchosauroides* footprints and the feet of *Rhynchosaurus* as restored by Smith Woodward (1907). But closer inspection shows that nearly all the footprints were made by long-legged, slender-toed reptiles. whereas *Rhynchosaurus* is comparatively short-legged and broad-toed as a modification for aquatic life. At this point it may be illuminating to note that in the same year in which he proposed the *Rhynchosaurus* correlation Owen was asserting, on essentially similar grounds, that *Chirotherium* footprints represented *Labyrinthodon.* The great contrast (now understood) between the feeble-limbed, bottom-crawling *"Labyrinthodon"* and the upright-limbed, semi-cursorial *Chirotherium* points up the ecological unsoundness of both correlations: the genera common in the Keuper bonebeds represent an aquatic facies-fauna while the footprints record a terrestrial facies-fauna.

Among terrestrial rhynchocephalians we may eliminate the Rhynchosauridae because of their un-lacertoid proportions and short, heavy phalanges. The Sphenodontidae, however, offer closer comparisons. Proportions similar to those of the Milford trackmaker are found in the Upper Jurassic *Homoeosaurus;* the Manchurian sphenodontid *Monjurosuchus* (Endo, 1940) is rather similar in manus structure (Figure 9 E) although its body proportions suggest that the pes probably did not overstep the

[10] Bock's attempt (1952, p. 422) to synonymize *Rotodactylus* with the araeosceloid Lower Permian footprint *"Ichnium gampsodactylum"* — more correctly termed *Dromopus* [*Saurichnites*] *lacertoides* (Geinitz), n. comb. — overvalues the apparent similarities at the expense of fundamental differences in foot structure and trackway pattern.

manus as much as in *Rhynchosauroides hyperbates*. Upper Triassic genera are (at this writing) less completely known, but the limbs of *Polysphenodon* compare favorably (as Huene points out) with footprints of the *Rhynchosauroides* type from the Keuper of Italy. As shown in Figure 9 F, the phalangeal pattern of *Polysphenodon* also corresponds approximately to that of the larger Milford lacertoid. The publication of current research on several skeletons of *Glevosaurus*, a sphenodontid from Keuper fissure fillings in Gloucestershire (Robinson, 1955), may well provide the means to a better understanding of *Rhynchosauroides*.

Triassic Lacertilia, a group in which major advances in knowledge are in progress, may similarly prove to correlate with some of the lacertoid trackways which I have brigaded under the name *Rhynchosauroides*. On the evidence now available *R. hyperbates* is assigned tentatively to the sphenodontid Rhynchocephalia, but lacertilian origin remains a distinct possibility. At present the various trackways cited above constitute the only evidence of rhynchocephalians or lacertilians in the North American Triassic.

CORRELATIVE AGE OF THE MILFORD FAUNULES

Research on several problems of Pennsylvanian and Permian ichnology, still unpublished, indicates that fossil footprints — especially footprint faunas — can be used in a limited way for stratigraphic correlation. As footprint species can at best be equated only with generic units of tetrapods they cannot approach the diagnostic precision of skeletal remains. Assemblages of footprints are of course subject to the same ecological bias as assemblages of skeletons, and may be equally deceptive in suggesting the non-contemporaneity of beds which are actually equivalent in age.

Despite such limitations ichnological evidence can be a valid basis for correlation; indeed, it is sometimes the only basis available. One pertinent example is the presence of similar *Chirotherium barthii* faunas in the Bunter of Germany and the Moenkopi of Arizona, which (with other evidence) establishes the equivalence of these strata. Consequently when a specimen of *C. barthii* which is indistinguishable from the Arizona ma-

terial appears (under the name *"C. higuerensis"*) in so-called Upper Permian beds of Argentina (Rusconi, 1951) we need feel no doubt that the beds are in fact Triassic.[11]

The amount of material now available and the size and diversity of the combined Milford faunules justifies an attempt at correlating them with faunas of other areas. In this assay footprints will be compared with footprints and bones with bones: for in the past, uncritical herpetological interpretations of misidentified and unanalyzed footprints have too often proved misleading in stratigraphic work.

Two views on the correlative age of the Milford footprints have been advanced: one, that the footprint assemblages of Milford and Whitehall, New Jersey, York Springs, Pennsylvania, and Aldie, Virginia, compare closely with the youngest footprint fauna of the Portland formation in Massachusetts (Bock, 1952, pp. 429-430); the other, that the Milford faunules correlate neither with the Portland nor the underlying Meriden but with the New Haven, lowermost of the Connecticut Valley formations (Baird, 1954, pp. 184-187). Let us examine these faunules, beginning with the southernmost.

The only specimen from Aldie available to me (MCZ 236) is a well-preserved pes imprint, 35 cm. long including the hallux, of *Anchisauripus tuberosus* (Hitchcock). This species ranges from the lower Meriden to the upper Portland formation. Of the Aldie fauna Gilmore (1924) says:

> "Three-toed imprints predominate though they vary in size from a length of three to fourteen inches. A few tracks were noticed having four toes, evidently terminated with wide, flat unguals. All of these are probably of dinosaurian origin, but a few small 4- or 5-toed tracks with traces of sharp claws perhaps pertain to some other group."

Until this important assemblage has been thoroughly studied no valid comparisons can be made.

Specimens from the Gettysburg shale of the Trostle stone quarry near York Springs, Adams County, Pennsylvania, are figured by Stose and Jonas (1939, pl. 22); others are preserved at the Carnegie Museum. In addition to invertebrate trackways

[11] Since the foregoing was written Peabody (1955) has published the same observation and noted the importance of this evidence on Triassic faunal distribution.

and some indeterminate vertebrate tracks the faunule contains three genera: (1) a uniquely quadrupedal dinosaurian type resembling *Anchisauripus gwyneddensis* Bock from the Lockatong formation, (2) a *Rhynchosauroides* (Figure 9 D) comparable to those from the Brunswick of Schwenkville and Milford and the Lockatong of Phoenixville, and (3) large footprints consisting of a sub-circular plantar pad close behind an arc of broad ungual depressions, rather suggestive of a dicynodont foot. Nothing like any of these forms occurs in the Connecticut Valley.

The Whitehall footprints are known to me only from the thoroughly unreliable faunal list of C. H. Hitchcock (1889). Further discussion is useless until the material can be restudied by modern methods.

Only one of the Milford species, *Anchisauripus parallelus,* also occurs in the Connecticut Valley. The other dinosaurian tracks are distinctly different from those of the Meriden and Portland formations. *Chirotherium* footprints, which at Milford record three genera of pseudosuchian reptiles, are unknown in New England; so are trackways of the *Apatopus* and *Rhynchosauroides* types. Their absence there is real and cannot be explained as the result of inadequate collecting or superficial study — far from it! In the absence of any evidence of barriers between the New Jersey-Pennsylvania basin and the ancient Connecticut Valley trough, the conclusion presented in my previous paper seems inescapable: the footprint beds of the upper Brunswick formation at Milford, New Jersey, antedate the Portland and Meriden formations and more probably correlate with the New Haven arkose of Connecticut. The most comparable footprints in the European sequence occur in formations of the middle to upper Middle Keuper of Germany.

REPTILES OF THE BRUNSWICK FORMATION

To recapitulate, the Milford footprints comprise three mutually exclusive faunules from three horizons of the Brunswick formation. What these footprints signify in herpetological terms is summarized, so far as known, in Table 3. These footprints probably represent only a few of the different types of reptiles which inhabited the area, and the reptiles themselves only a segment of the biota. Nevertheless a partial account of the

TABLE 3

MILFORD FOOTPRINT FAUNULES WITH PRESUMED REPTILIAN EQUIVALENTS

HORIZON	SPECIES	INTERPRETATION	INDIVIDUALS
Reddish-brown siltstone	*Chirotherium lulli*	Small ornithosuchid pseudosuchian, cf. *Euparkeria*	1
	cf. *Coelurosaurichnus*	Small coelurosaur or ?tridactyl pseudosuchian	1
	cf. *Anchisauripus gwyneddensis*	Small dinosaur	1
Level A	*Grallator sulcatus*, n. sp.	Coelurosaur, cf. *Coelophysis*	Several
Level B Gray shale & sandstone at Levels A and B	*Anchisauripus milfordensis*	Coelurosaur	3+
	Anchisauripus parallelus	Coelurosaur	1
	Genus incertum	Small dinosaur	1
	Chirotherium parvum	Large pseudosuchian	3
	Chirotherium eycrmani, n. sp.	Large pseudosuchian	1
	Apatopus lineatus, n. gen.	Phytosaur, cf. *Clepsysaurus*	5-6
	Rhynchosauroides hyperbates, n. sp.; *R.* sp.	Sphenodontid rhynchocephalians or lacertilians	2, 3+

Brunswick fauna and its ecological relationships can be formulated from the known footprints and bones.

Faunal content. In the preceding attempts to determine the zoological positions of the trackmakers, failure to achieve a correlation between footprint and reptile has been due less often to inadequacy of the footprint material than to lack of comparable skeletal material. This lack is twofold in origin. First, the Triassic reptiles as known are largely a spectral crew of footless bodies and disembodied heads which can be made whole only by persistent and lucky collecting. As our knowledge of these forms increases, closer comparisons with the tracks will no doubt become possible. Second, and more fundamental than the fragmentary preservation of individual taxa, is the fragmentary and selective preservation of the original fauna. At present we know more types of Brunswick tetrapods from their footprints than from skeletal material. Aside from a dinosaur leg excavated by laborers but never collected (Colbert, 1946, p. 231), the only genera known are the metoposaurid amphibian *Eupelor,* the procolophonid cotylosaur *Hypsognathus,* the phytosaur *Clepsysaurus,* and the aëtosaurid pseudosuchian *Stegomus.*

Other Brunswick footprint assemblages — e.g. from Sanatoga and Collegeville, Pennsylvania, and Tumble Falls and Whitehall, New Jersey — which would augment the fauna have been omitted here because of the unreliability of old identifications. Figured specimens of *Anchisauripus* [*"Otouphepus"*] *poolei* (Bock) and *Rhynchosauroides* [*"Orthodactylus"*] *howelli* (Bock) from Schwenkville, Pennsylvania, which Wilhelm Bock has kindly made available for study are specifically indeterminate but appear to record a coelurosaur and a lacertoid reptile of sphenodontid aspect. The Schwenkville *"Grallator cuneatus"* (Bock, 1952, pl. 45, fig. 1) is surely not that genus but instead has the phalangeal pattern of *Anchisauripus;* it evidently represents another variety of coelurosaur.

Ecology. The Brunswick fauna is predominantly terrestrial but includes representatives of the aquatic biotope in the form of metoposaurs and phytosaurs. These were certainly fish-eaters and presumably fed on the coelacanths, semionotids, dictyopygids and palaeoniscids of the Newark lakes and streams. The presumed sphenodontid rhynchocephalians of Level B may (like

Homoeosaurus) also have fed occasionally on fish, but the bulk of their diet (like that of *Sphenodon*) probably consisted of insects, other arthropods, grubs, and small tetrapods. Except for the cotylosaur *Hypsognathus,* a presumed herbivore, the other known members of the fauna were carnivorous. Lacertoids and procolophonids furnished food for small, agile pseudosuchians of the *Chirotherium lulli* type, and all three groups formed the prey of the raptorial coelurosaurs. Whether the larger Milford pseudosuchians were predators or carrion-feeders, or both, cannot yet be determined.

Any assessment of the Brunswick ecology must allow for a disproportionate percentage of aquatic animals in the skeletal record; the footprint horizons, on the other hand, record a more representative proportion of terrestrial genera. More important, the footprint faunules constitute biocoenoses in a strict sense, while the skeletal remains occur as isolated finds or (at best) as bonebed thanatocoenoses of animals which may or may not have formed natural communities in life. Thus we can say with confidence that the reptiles of Level B, for example, constituted an animal community which occupied the Milford mudflat during a period measured in days. Our sample is too small, unfortunately, to furnish significant data on the numerical composition of the faunules.

Survey of the Newark tetrapods. Undoubtedly the assemblage described above is only a fraction of the actual tetrapod fauna of Brunswick time. To afford a clearer perspective, the known terrestrial vertebrates of the entire Newark province are listed with the Milford trackmakers in Table 4.

How incomplete this faunal picture remains may be deduced from the many reptiles and amphibians, both genera and higher groups, which are known from the Upper Triassic of Arizona, Utah, New Mexico, Texas and Wyoming. Among these are the metoposaurid amphibian *Eupelor* [=*Buettneria, etc.*] (Colbert and Imbrie, 1956), the large protorosaur *Trilophosaurus,* a variety of phytosaurs, the armor-plated pseudosuchians *Desmatosuchus* and *Typothorax*, the little ornithosuchid pseudosuchian *Hesperosuchus*, the coelurosaur *Coelophysis,* and the dicynodont *Placerias.* Many of these forms (or their relatives) must have inhabited the Newark depositional area. Still other types of

tetrapods yet unknown, small forms in particular, completed the fauna.

It would obviously be premature to attempt here a reconstruction of late Triassic tetrapod faunas in space and time on the basis of skeletal and ichnological data now available. This is a major project to which several researchers are individually contributing, and in which the collaboration of invertebrate paleontologists, paleobotanists, and geologists is essential. Nevertheless the present study may serve to illustrate the contribution which one field of investigation, ichnology, can make to the solution of the general problem.

APPENDIX I: THE NATURE OF OTOUPHEPUS

A study of the type specimen of *Otouphepus magnificus* Cushman, lent through the courtesy of the Museum of Science, Boston, suggests that it is not the direct imprint of a foot but rather an impression transmitted to a surface some millimeters below the one on which the animal walked. This circumstance has softened the outlines and produced the illusion of a compact foot in which the digits were firmly united and surrounded by a web. The dark-colored web outline described by Cushman (1904, p. 155) proves to be a thin coat of gum which was readily removed with soap and water. Analysis of the pattern of articular pads reveals a pedal structure which is well within the limits of *Anchisauripus*. A previously undescribed claw-mark occupies exactly the position of an *Anchisauripus* hallux imprint.

The only plesiotype cited by number (Lull, 1953, p. 177) is morphologically indistinguishable from *Anchisaurus tuberosus* — a fact which Lull has pointed out in recent correspondence.

In size and skeletal structure the unique specimen of *O. minor* Lull (1915, p. 190) is a typical *Grallator;* its peculiarities are readily explained as artifacts of impression. (Latex molds of the two preceding specimens were kindly furnished by the Yale Peabody Museum.)

A third species, *O. poolei* Bock (1952, p. 407) has been based on an obscure and isolated footprint from the Brunswick formation near Schwenkville, Pennsylvania. With Wilhelm Bock's gracious permission this specimen has been latex-molded and

TAXA	SKELETAL REMAINS	MILFORD TRACKMAKERS (as genera) (B)
AMPHIBIA		
Stereospondyli:		
Metoposauridae	*Eupelor* [*Calamops*] (S, G)	
	Dictyocephalus (DR)	
REPTILIA		
Cotylosauria:		
Procolophonidae	*Hypsognathus* (B)	
Rhynchocephalia (?)		2 ?sphenodontids
Pseudosuchia:		2 large pseudosuchians
Ornithosuchidae	*Stegomosuchus* (P)	1 ?+ ornithosuchid
Aëtosauridae	*Stegomus* (B, NH)	
Phytosauria	*Clepsysaurus* (L, B, G, PD, NH)	1 cf. *Clepsysaurus*
	Rutiodon (DR, ?G)	
Coelurosauria:		3+ coelurosaurs
Ammosauridae	*Ammosaurus* (P)	
Podokesauridae	*Podokesaurus* (P)	1 cf. *Coelophysis*
Prosauropoda:		
Thecodontosauridae	*Yaleosaurus* (P)	
	Thecodontosaurus (L, P)	
Cynodontia	*Dromatherium* (DR)	
	Microconodon (DR)	
INCERTAE SEDIS	*Gwyneddosaurus* (L)	
	Lysorocephalus (L)	

analyzed. An apparent structural formula of B, B, C, C allies this species with the *Anchisauripus tuberosus-exsertus-parallelus* species group. The species is probably distinct, but in the absence of adequate material its small size is the only characteristic which cannot be attributed to impression phenomena.

If *Otouphepus* Cushman (March, 1904) and *Anchisauripus* Lull (April, 1904) are synonymous the former takes priority. To abandon a well-established name which has been applied to several species comprising thousands of specimens, in favor of a name which has been applied to four specimens whose chief point of similarity is their obscurity, would be unreasonably legalistic. I have therefore (Baird, 1956) petitioned that the International Commission for Zoological Nomenclature exercise its plenary powers to suppress *Otouphepus magnificus* as a *nomen dubium;* this action automatically entails the suppression of Lull's family Otouphepodidae. At the same time *Anchisauripus sillimani* and the family name Anchisauripodidae are to be placed on the official lists of names in zoology as *nomina conservanda.*

APPENDIX II: BRONTOZOUM

The generic name *Brontozoum,* formerly applied to a number of species of theropod footprints from the Newark series, was erroneously reduced to synonymy in Hay's 1902 bibliography. In his monograph of 1904 Lull followed Hay's usage, and since that time the name has been in disuse. *Brontozoum* nevertheless remains a valid prior generic name for the type species of *Anchisauripus* Lull, and could legally be revived to replace that well-known generic name. The facts are as follows:

Brontozoum Hitchcock, 1847, was proposed to include "five" species of which only three were cited by name: the new species

TABLE 4. SURVEY OF THE NEWARK TETRAPODS

Formations: Deep River coal measures (**DR**) of North Carolina; Stockton (**S**), Lockatong (**L**), Brunswick (**B**) of Pennsylvania-New Jersey basin; Gettysburg shales (**G**) of York County, Pennsylvania (Wanner, 1926); bed below Palisades diabase (**PD**) of New Jersey; New Haven (**NH**), Meriden, Portland (**P**) of Connecticut Valley.

parallelum,[12] *sillimanium* (an invalid emendation of *sillimani*, 1843) and *giganteum*. No type species was designated. No subsequent author, to my knowledge, has designated a type species, so all three remain available.

A case of sorts could be made for the selection of *parallelum* through a broad construction of Article 30 A(a)(ii) of the International Rules of Zoological Nomenclature, which provides that the expression "n.g., n.sp.," can constitute a designation of type species. In this case such a construction is highly dubious, particularly as it cannot be claimed to represent the intent of the original author: for Hitchcock evidently had no intention of designating a type species for any of his footprint taxa. Furthermore, *parallelum* is based on two specimens — neither designated as type — which are not conspecific. My analysis assigns one of these (Hitchcock's fig. 2 b) to *Anchisauripus sillimani* and the other (fig. 2 a) to *Grallator tenuis*. To avoid confusion I designate the specimen represented by fig. 2 b as the type of *parallelum*, and reduce this species to subjective synonymy with *sillimani*.

The second species, *Brontozoum sillimani*, is the type species of *Anchisauripus* Lull, 1904 (see Baird, 1956, paragraph 6). Lull clearly erred in erecting a new genus with a type species for which the name *Brontozoum* was available.

The third species originally assigned to *Brontozoum*, *B. giganteum*, was first described by Hitchcock (1836) as a species of *Ornithichnites* and was later transferred by him to *Eubrontes* (1845) and to *Brontozoum* (1847). In 1902 Hay designated it as the type of *Eubrontes*.

Since according to Article 30 B(g)(i) of the International Rules the designation of a species as the type of one genus does not in itself preclude the selection of that species as the type of another genus, either *sillimani* or *giganteum* is eligible to be the type species of *Brontozoum*. If *sillimani* be selected then *Anchisauripus* (1904), an important name accepted for more than fifty years, must be replaced by *Brontozoum* (1847), a name generally rejected or ignored during the same period. If *giganteum* be selected, however, then *Brontozoum* becomes a

[12] This species *B. parallelum* is not to be confused with *Anchisauripus* [*Grallator*] *parallelus* (Hitchcock, 1865) although Hay (1902, p. 545) did so confuse it.

junior objective synonym of *Eubrontes* (1845) through the identity of their type species.

I therefore designate *Ornithichnites giganteus* Hitchcock, 1836, as type species of the nominal genus *Brontozoum,* thereby synonymizing that genus with *Eubrontes.* This suppression of *Brontozoum* serves to maintain the familiar nomenclature of Lull's classic monographs of 1915 and 1953 which have done so much to bring nomenclatural stability into a confused field.

SUMMARY

Problem and method. Quarries in the Delaware valley near Milford, New Jersey, have yielded three faunules of reptile footprints at three horizons of the upper Brunswick formation (Newark series, Upper Triassic). Each determinable species was analyzed by comparison of outlines printed from latex molds of all adequately preserved specimens. Body proportions and locomotor habits of the trackmakers were deduced from trackways (where available) and the pedal skeletons were reconstructed from the arrangement of articular swellings in the footprints. Comparison with other Triassic footprints furnished data on faunal distribution and stratigraphic correlation; comparison of the restored skeletons with those of Triassic reptiles served to elucidate and enlarge the known Brunswick fauna.

Reddish-brown siltstone layer. The youngest faunule (discussed in a previous paper) records three reptilian genera as footprint species: an indeterminate small dinosaur, another resembling *Coelurosaurichnus* (sensu stricto) of the German Middle Keuper and the Gettysburg shale of Pennsylvania, and an ornithosuchid pseudosuchian, *Chirotherium lulli* Bock, the last-known member of its genus. This faunule and that of Level B are the only American *Chirotherium*-dinosaur associations known.

Level A (gray sandstone over shale). *Grallator sulcatus,* n. sp., a small dinosaur with digits II-III united and IV independent, is less digitigrade than its Connecticut Valley congeners. Among coelurosaurs the massive German *Halticosaurus* (as shown by pedal reconstruction) made footprints resembling *Eubrontes;* little *Procompsognathus* compares more closely with

Grallator, especially *G. cursorius;* and *Coelophysis* correlates approximately with *G. sulcatus.*

Level B (gray sandstone over shale). Three dinosaur genera occur: *Anchisauripus milfordensis* (Bock), a broad-based footprint without functional hallux, found also in the Gettysburg shale of York County, Pennsylvania; *A. parallelus* (Hitchcock), only 6/11 the size of conspecific New England footprints; and an enigmatic small form of York County affinities. Taxonomic placement follows a new type of key based on relative positions of phalangeal and metatarso-phalangeal joints. Re-analysis of various Upper Triassic theropod tracks by this method necessitates reassignment of several species and emphasizes the similarities between *Grallator* and *Anchisauripus* (sensu stricto), genera previously considered familially distinct but here united as Grallatoridae and correlated with coelurosaurian dinosaurs.

Two large chirotheriids with hoof-like fifth pes digits represent a lineage previously known only from the German Middle Keuper, here designated the brachychirotherian group. In *Chirotherium parvum* (C. H. Hitchcock) (=*C. copei* Bock), narrow claws on pes digits I-III were carried well above the distal pad and directed obliquely laterad; pes digit I was robust. In the new species *C. eyermani* straight, heavy claws I-IV lay at sole level and digit I was weak. Skeletal reconstructions of the large-manus *C. barthii* (cosmopolitan, Lower Triassic) and the small-manus *C. lomasi* (Keuper of England) contrast with those of the Milford brachychirotherians. All three Milford chirotheriids show parallel evolutionary tendencies — characteristic of late Triassic species — toward functional tetradactyly through elimination of lateral propping function in pes digit V. Inefficient locomotion and increased dinosaurian competition probably contributed to the extinction of *Chirotherium.* Pseudosuchians correlative with the large Milford species are unknown.

Discovery of additional material permits redescription of *"Otozoum" lineatus* Bock as a new type of footprint, *Apatopus* n. gen., correlated with a phytosaur such as *Clepsysaurus* — the first phytosaur footprints known. Crocodilian in trackway pattern except for the forward-turned manus, *Apatopus* differs from all crocodilians in its long fourth and functional fifth pes digits. Webs apparently connected the claw bases. Both adults

and juveniles are represented, one adult having a gleno-acetabular length of 52 cm.

Lacertoid footprints of the genus *Rhynchosauroides* [*Akropus*] occur in the Brunswick, Gettysburg, and Lockatong formations of Pennsylvania-New Jersey, the Dockum of New Mexico, and the Keuper of England and Italy. *Rhynchosauroides hyperbates,* n. sp., represents an agile reptile some 75 cm. long with a gleno-acetabular length of 18 cm. Pes regularly overstepped manus, and both were digitigrade with the metapodio-phalangeal joints carried clear of the ground. A smaller Milford species is inadequately known. Affinities appear to lie with the sphenodontid Rhynchocephalia or the Lacertilia.

Correlative age. The Milford faunules are akin to those of the Pennsylvania-New Jersey basin and the German middle to late Middle Keuper but not (as sometimes held) to the familiar footprint assemblages of the Portland and Meriden formations of New England. Only one of the dinosaurian species also occurs in the Connecticut Valley; while *Chirotherium, Apatopus,* and *Rhynchosauroides* are definitely absent from the abundant and thoroughly studied Portland and Meriden faunas. No topographic or ecologic barriers would seem to have prevented interregional migration. Presence of the phytosaur *Clepsysaurus* and the pseudosuchian *Stegomus* in the lowest formation (New Haven arkose) of the Connecticut Trias as well as in the Brunswick formation, and the possible correlation of the three episodes of igneous extrusion in New Jersey with the three lava flows of Meriden time, suggest that the Brunswick antedates the Portland. The Milford footprint beds of the upper Brunswick appear to correlate best with the New Haven arkose.

Reptiles of the Brunswick formation. Known skeletal remains include undetermined dinosaurs, the cotylosaur *Hypsognathus,* the aëtosaurid pseudosuchian *Stegomus,* and the phytosaur *Clepsysaurus.* To this fauna the Milford footprints add three or four types of coelurosaur, one small ornithosuchid and two large undetermined pseudosuchians, a phytosaur, and two lacertoids. From these combined faunal lists the ecological picture may at least be glimpsed, though only a fraction of the Brunswick fauna is yet known. The present study serves to illustrate the possible contribution of ichnology to the solution of Triassic faunal and stratigraphic problems.

Appendix I. The nominal genus *Otouphepus* proves to be a catch-all for obscurely preserved dinosaur footprints. Its suppression as a *nomen dubium* is proposed in order to prevent possible displacement of *Anchisauripus* as a junior synonym.

Appendix II. The long-disused name *Brontozoum* also threatens the stability of the later name *Anchisauripus*. *Brontozoum* is therefore cashiered by the designation of a type species which is also the type species of the earlier genus *Eubrontes*, so that the genera become objectively synonymous.

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PLATES

PLATE 1

Fig. 1. *Grallator sulcatus* Baird, n. sp. Type, MCZ 215, a left pes imprint. (As all specimens are natural casts, left and right appear reversed.) Fig. 2. *Chirotherium parvum* (C. H. Hitchcock). Left manus-pes set, a composite of MCZ 209 (pes) and MCZ 210 (manus).

PLATE 1

PLATE 2

Chirotherium eyermani Baird, n. sp. Three views of the type, MCZ 134, a left pes imprint. Note the furrows along the lateral border of hoof-like digit V.

PLATE 2

PLATE 3

Apatopus lineatus (Bock). Fig. 1. Right manus-pes set of the type individual, MCZ 212. Pes digits IV and V failed to impress. Fig. 2. Well-preserved left pes imprint, MCZ 213. Obliquely left of claw II is a manus print of *Rhynchosauroides* sp. (cf. Figure 9 C).

PLATE 3

PLATE 4

Apatopus lineatus (Boek). Fig. 1. Juvenile left manus-pes set, MCZ 214; note the beaded squamation. Fig. 2. Juvenile left pes imprint, AMNH 2259, rotated after implantation. Fig. 3. Small right pes imprint, AMNH 2258.

PLATE 4